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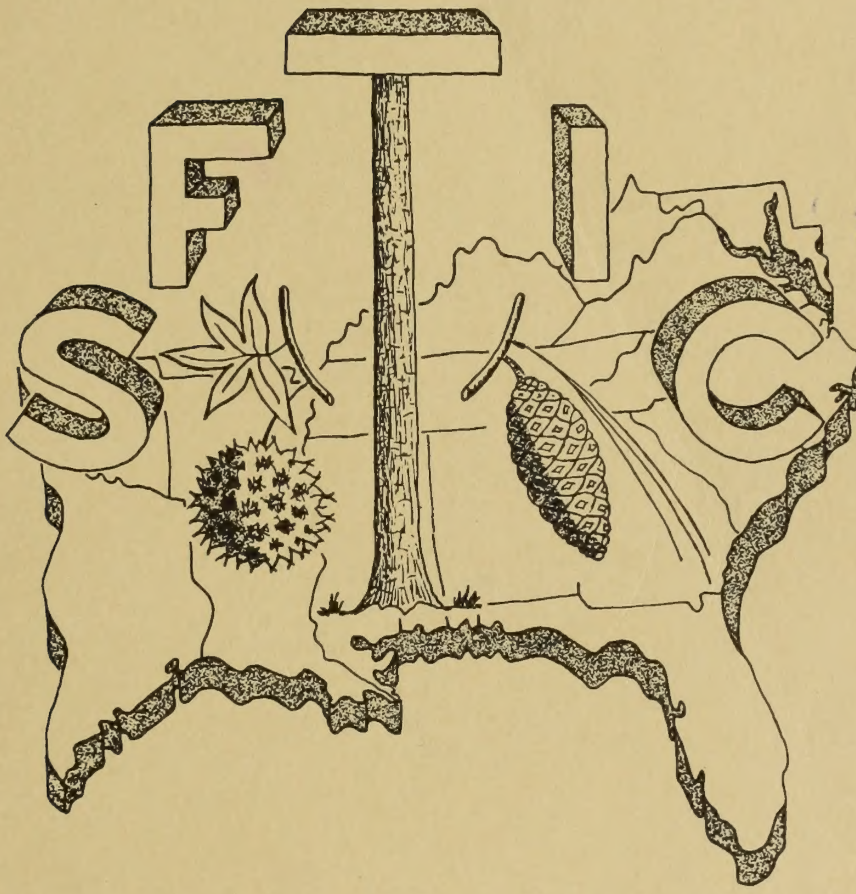

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THEME: The Impact of Tree Improvement on Forestry in the South

Sponsored by
THE SOUTHERN FOREST TREE IMPROVEMENT COMMITTEE
JUNE 19-21, 1979
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PROCEEDINGS OF THE

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FORWARD

The Fifteenth Southern Forest Tree Improvement Conference was held in the Dorman Hall Auditorium on the campus of Mississippi State University in cooperation with:

The Department of Forestry
Mississippi State University

and

The Southern Forest Experiment Station
USDA Forest Service

Conference Co-chairmen

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Department of Forestry	USDA Forest Service
Mississippi State University	Southern Forest Experiment Station

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TREE IMPROVEMENT IN THE SOUTH -- A PROMISE FULFILLED

John C. Barber[1]

Abstract.--Highlights the initiation and successes of tree improvement programs in the South.

Mr. Chairman, ladies and gentlemen, I am happy and honored to participate in this 15th Southern Forest Tree Improvement Conference. Throughout my professional career I've had strong ties with tree improvement in the South. For many years I was an active participant and for many years after that I directed some of the Forest Service work from Washington and New Orleans. With this background I want to comment on some of the events that have led to a remarkable performance and accomplishments that have not been matched in the history of American forestry.

The Early Years

Tree Improvement has been discussed by American foresters since the turn of the century, but nothing much happened until World War II. It was only then that conditions were ripe for major and concerted advances in tree improvement. Efforts initiated in the 40's triggered the major initiatives of the 1950 decade. The Southern Forest Tree Improvement Committee played an important role in these rapid advances. However, there were significant developments in the South that took place earlier and are worthy of note.

In 1927, Phil Wakeley of the Forest Service's Southern Station established the first loblolly pine seed source study at Bogalusa, LA. His interest in geographic variation was carried over from college days and an interest in hybrids was whetted by H. H. Chapman's description of Sonderegger pine. Thus, in 1929, he made the first artificial longleaf x slash pine cross, and 2 years later he backcrossed Sonderegger pine with loblolly and with longleaf pollen. Wakeley did this work outside office hours because Washington overhead disapproved. I quote from Phil's "Biased History of the Southern Forest Experiment Station" written in 1964: "I was criticized for dissipating my efforts even on my own time. Yet, after the hybrids were published by Ernest Schreiner in the 1937 Yearbook of Agriculture, the same man who voiced the criticism wanted to know why the hell I hadn't made more of them!"

In 1934, Lee Chaiken helped design a progeny test with loblolly pine in South Carolina involving 105 half-sib families. Leon Minckler (1942) reported significant differences between families in survival and height growth. After 4 years in the field, however, the test was lost by flooding.

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[1] Associate Deputy Chief, U. S. Forest Service, Washington, DC.

In 1936, Ted Liefeld established the first gum-yielding test with longleaf pine. He planted open-pollinated progeny of above-average and of below-average yield. Seventeen years later, Francois Mergen obtained from this test the first definite proof that gum-yield is inherited.

In 1942, during World War II, in Olustee, Florida, a pioneer in tree improvement, Keith Dorman quietly laid the ground work for a naval stores genetics program in slash pine. Before retirement a few years ago Keith wrote the definitive book on genetics and breeding of Southern pines, a fitting final statement in an outstanding career.

Keith's enormous impact on forest genetics in the South belies his apparent frail physique and unassuming manner. For those who know Keith it is hard to imagine that in the early days he built a device of 3 two by fours to brace the very tip of the tall slash pines he climbed so as to pollinate even the uppermost flowers. Thus, Keith established the first true progeny test of known parentage in the South. In those years also, he established the first clonal test from rooted cuttings.

The several hundred offspring from Dorman's controlled crosses and the rooted cuttings plantation furnished the basis for many of the best and most important publications in forest genetics in the 1950's.

In retrospect, these studies appear somewhat amateurish. A couple of hundred crosses, a few dozen rooted cuttings, an acre of provenance test seem small efforts today. They were, however, the stuff that made silviculturists become tree breeders and forest geneticists, and also the stuff that persuaded administrators to fund tree improvement programs.

Cason Callaway, philanthropist, was stimulated by an article he read about southern pine hybrids at the Institute of Forest Genetics, Placerville, California. He financed a project to breed pines to improve Georgia's forests and economy. Under the supervision of Keith Dorman, then at Asheville, Callaway financed work at Callaway Gardens and employed a full-time forester, Jim Greene. Though the financing ceased years ago, Callaway plantations provided much early inheritance information, and perhaps more important, they provided a vivid visual demonstration of the inheritance of many economically important traits of the Southern pines.

There were several events that contributed to the formation of the Southern Forest Tree Improvement Committee (SFTIC). One was the English translation of Bertil Lindquist's "Genetics in Swedish Forestry Practice." Another was the attendance of several prominent American foresters at the Third World Forestry Congress in Helsinki in 1949. Ted Haig, Herb Stone and Len Barrett of the Forest Service were impressed by the forest genetics work in Northern Europe and promoted forest genetics research upon their return.

In 1951, the first Southern Forest Tree Conference was held in Atlanta. Attendance at the conference was expected to be around 25 but nearly 3 times that number showed up to the surprise of the organizers. Ever since that first meeting the work of the Committee has been characterized by deep interest, great enthusiasm, and unstinting, voluntary cooperation by people and organizations. But as some of the "old timers" know, the meetings were not always without emotional argument and sometimes confrontation. In the end, however, the overriding desire to improve Southern forest always dominated. Many were the debates on how much gain to expect and to predict in promoting tree improvement.

Through the years, the Southern Forest Tree Improvement Committee has continued to play its vital role of coordinating activities, sponsoring publication of research results, and providing a forum where tree improvement workers can meet and mingle. Let no one underestimate, however, its sense of mission and its promotion in the early years of public and private funding of tree improvement research and development. This may well have been the Committee's most telling impact. Its conferences were each a landmark in reporting new knowledge - the South having the great advantage of early juvenile growth of its pine species.

The success of the committee inspired the organization of similar groups around the Nation: in the Lake States in 1953, in the Northeast and in Canada in the same year, in the West in 1954, in the Central States in 1958, and in the Rocky Mountains in 1978.

In 1951, the Southwide Pine Seedsource Study was started. Organized by Phil Wakely under auspices of SFTIC it was the first, truly large scale U. S. effort in provenance research and a marvel of cooperation.

You must remember that times were lean in the early fifties. Phil Wakely had $62 for equipment the year he organized the study. The entire 136,000 tree study was put in with the help from cooperators drawn from industrial corporations, State organizations, schools of forestry, and federal agencies.

In 1951, Texas A&M and the Texas Forest Service organized a tree improvement program under the direction of Bruce Zobel. At first the program was strongly research oriented; later the program was reorganized, with emphasis on technical assistance and cooperation, into the Western Gulf Forest Tree Improvement Program carried out by the present 18 members. Claud Brown and Hans Van Buijtenen got their start here.

In 1953, the Southeastern Station began funding forest genetics research at Lake City, Florida, following up on Dorman's earlier work.

Prominent researchers in the early years of that program were Tom Perry, Francois Mergen, Tony Squillace, and Ed Merkel.

The Southeastern Station also started a tree improvement program in Macon, Georgia in 1954 in cooperation with the Georgia Forest Research Council and the Georgia Forestry Commission. That project, under Keith Dorman, already had established ties with the earlier work of the Callaway Foundation, and Bratislav Zak's work on pine grafting and resistance to little-leaf disease at Athens. The Georgia Forestry Commission launched its major seed orchard effort that year.

In 1954, the University of Florida Forest Tree Improvement Program was started under the direction of Tom Perry and Chi-Wu Wang. This was the first of the University Cooperatives with direct participation of the 7 cooperators in research and development, with the objective of providing seed orchards for each cooperator.

In 1955, the Southern Institute for Forest Genetics was dedicated and placed under the direction of Berch Henry. Prominent researchers in the early years were Bayne Snyder, Fred Jewell and Ossie Wells. The Institute was to do fundamental genetics research for application region-wide, and tree improvement studies of an applied local nature. It built on, and eventually assumed the earlier studies of Phil Wakeley.

In 1956, the North Carolina State - Industry Cooperative Tree Improvement Program was organized under the direction of Bruce Zobel. Starting out with 11 members, this has become the largest of the Cooperatives with 32 working units in the pine program and 22 working units in the hardwood program. The cooperative is loosely organized with no charter, written rules or regulations. An advisory committee with a representative from each cooperator meets yearly to receive a report and give guidance.

The year 1956 seems a good year to cut off this list of early initiatives. I've hit only a few of the highlights, and have done grave injustice to individual contributions and to important programs, large and small, that have appeared since 1956. However, I wanted to show how and where the foundation was laid for the present effort in southern tree improvement. Today the South has a total of some 10,000 acres in seed orchards, has started establishment of advanced generation seed orchards, and the various programs encompass all Southern pines and some 2 dozen hardwood species.

The impetus to undertake tree improvement was driven by the enthusiasm and confidence in success of people like Wakeley, Dorman, Ostrom, Zobel, Kaufman, Weisehuegel and Callaway. State foresters like Guyton DeLoach in Georgia, Al Folweiler in Texas, and Hux Coulter in Florida set the pace by committing substantial seed orchard initiatives built on promises but little proof - and as usual in the South, forest industries like Buckeye, IP, Union-Camp, Westvaco, St. Regis, Champion, etc. were waiting to put every piece of knowledge to work.

Impact

While nearly every paper on tree improvement in the early years held out promise of increased growth, straighter stems, greater disease resistance and more, the writers were careful never to predict just how much the characteristics could be improved in quantitative terms. An air of conservatism prevailed, lest the future be jeopardized by "snake-oil salesmanship." Tree improvement was never presented as a panacea--only a good silvicultural tool. Perry and Wang in a 1958 Journal of Forestry article came the closest to making quantitative predictions. They calculated the value of pine seed over a range of genetic improvement for growth. It is this range that is of interest to us now; 1/2 percent to 50 percent. Of course 50 percent was the timorous hope of all tree breeders at the time but the authors found it safer to show that even 1/2 percent gain was still worthwhile.

In 1963, at the 7th SFTIC in Gulfport, we had more data and more confidence. I say we, because I myself made these predictions at that time:

--4-6 percent gain in specific gravity
--2-3 percent reduction in compression wood
--10-15 percent gain in volume of wood.

Ray Marler, at the same conference, expected a 5 percent overall improvement in increased wood yields.

Frank Cech, also at Gulfport, cited Hans Van Buijtenen, who had more confidence than any of us then, with prediction of a 10 percent gain in specific gravity and in stem diameter from one cycle of selection. He believed that an increase of 25 percent in total wood production would not be out of reason.

These were modest predictions when compared to the actual gains that have been demonstrated since. Genetic gains expected today from first generation selection in slash and loblolly pines are roughly as follows:

Characteristic	Relative Gain
Volume	
1st generation seed orchard	10-20 percent
" " " " "(rogued)	15-25 "
1½ generation seed orchard	20-30 "
Specific Gravity	10 "
Straightness	50 "
Fusiform rust resistance	35 "
Oleoresin Yield	100 "

The impact of tree improvement on forestry in the South has been deep and strong. In seed procurement, for instance, drastic changes have taken place. As late as the early fifties, nurserymen would buy cones and seed of the desired species and not question where and what kinds of trees they came from. Today much of the seed comes from seed orchards, most of the rest is of the correct provenance and from trees with acceptable form. According to Zobel, the members of N.C. State Cooperative planted 500,000 acres with genetically improved stock this past season; every acre they planted![1] A whole new system of seed orchard management has grown up using selected and well-prepared sites, with fertilizer regimes, irrigation if needed, and elaborate systems of protection against insects and disease. The progress from flowering to cone and seed development is carefully monitored.

There is the Eastern Tree Seed Laboratory at Macon, Georgia, which provides, in addition to the usual seed testing and nursery services, Seed Orchard Seed Evaluation Testing, Cone Analysis Service, and a clearinghouse to expedite the sale of surplus seed, seedlings, and pollen.

Tree seed certification is now available in most Southern States, and is provided by a State agency. Recently the certification agencies in 7 Southern States have added the provision, on request, of international certification under the auspices of the Organization for Economic Cooperation and Development (OECD) with headquarters in Paris, France.

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[1] Zobel, Bruce J. Southern Forestry Conference, Forest Farmer Assoc.- Memphis, TN - May 1979 -

Nursery practices had to be developed to maintain the identity of the seed through growing, harvesting, shipping and planting the seedling. Certification programs can be carried through the nursery production and seedling distribution steps if desired. As we move ahead to several levels of improvement and emphasis on special traits, I can visualize a need for seedling certification to assure planters that they have the proper stock. The time may not be far off when seedling certification will be routine.

Tree improvement played an important role in the rapid expansion of tree planting in the South, focusing on site selection and preparation, seedling quality and planting technology.

At the first Southern Forest Tree Improvement Conference in 1951, Dr. I. T. Haig said that over 200 million trees were being planted annually in the South. Last year, nearly 900 million seedlings were planted and about 40 percent of these were genetically improved. A very quick and rough calculation shows that genetic improvement of last year's stock alone will add to the annual total yield in the year 2000 some 200 million cubic feet of wood. And that impact will grow even more spectacularly if present tree improvement efforts are continued.

A Look into the Future

The Southern Forest Tree Improvement Committee, in its 28th year, can look back on a role of inspired leadership, cooperation and coordination. It has not lost an ounce of its vigor or enthusiasm. I am sure that the Committee, as the art and practice of tree improvement develops, is looking to extend its activities in more directions. It is with this in mind that I offer the following remarks.

Until now, it has been taken for granted in the South that the benefits from tree improvement will accrue only through plantations. However, 2 factors may encourage us to think beyond the planting concept. (1) As tree improvement marches on and second generation and special purpose orchards come into production, there will still be an enormous volume of first, rogued, and 1½ generation orchard seed available. (2) The non-industrial private forest owner for various reasons is becoming more and more reluctant to invest in intensive site preparation and planting. Developing methods to establish stands of improved stock other than through complete site preparation and planting would be a welcome addition to Southern silviculture. We will have enough improved seed perhaps to use direct seeding at a modest cost.

Another area that needs attention in the South is seed, and perhaps, seedling certification. Although certification is offered in quite a few States, only if it is demanded by the buyer of seed will certification come into its own. With certification authority vested in the several State agencies that have an agricultural background, and a distant, rather low-key international certification scheme, the situation is made to order for the leadership and coordination of the Southern Forest Tree Improvement Committee. Exported seed should all be certified. We tend to think that we have adequate seed control and seedling distribution to proper sites -- perhaps, but I suggest the final step of certification to assure the public that their interest and environment are protected.

A third opportunity is in the area of gene conservation. Along with the large benefits derived from genetic manipulation, tree improvement workers assume a moral obligation to see that no irreparable harm is done to the gene pool and that genetic diversity is maintained. A rising tide of correspondence from concerned citizens on this subject with reference to National Forest management leads me to believe that it soon will become more than just a moral obligation.

Forest tree gene conservation is a complex subject. It is a matter of technology - far from perfect thus far - and of policy. It concerns the researcher as well as the practitioner of tree improvement. It involves all classes of ownership - from the Federal Government to the small private landowner. And let us not forget the public at large ready to render judement at the drop of a news article or commentary.

This opportunity for positive action is made to order for the unique talents and experience of the Southern Forest Tree Improvement Committee.

Assessing The Present

When I was still an active tree breeder, the SFTIC was a biennial highlight for me to visit other researchers, hear the latest, and get together on new cooperative ventures. I am looking forward to this one with the same enthusiasm.

Tree improvement in the South - A Promise Fulfilled - that is an understatment. We have far exceeded, perhaps not our wildest dreams, but certainly our best conservative calculations; those calculations that convinced the researchers and the managers of Southern Forests that tree improvement was real and a paying proposition. And there are still great payoffs to come, both in breeding progress and in the harvest, just now beginning, of the fruits of our efforts. Today when I walk through orchards, nurseries, and plantations and see the work accomplished during the span of my career, I'm proud of all of us in the South who have set the pace for World Forestry.

On the occasion of this, its 15th Conference I express the wish that the SFTIC may continue to be as vigorous, diverse, adaptable and long-lived as the pool of genes that makes the Southern forest unique in the world.

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PROGRESS AND FUTURE NEEDS OF FOREST GENETICS RESEARCH IN THE SOUTH

A. E. Squillace[1]

Abstract.--A broad view of forest genetics research in the South reveals some problems needing emphasis, and suggests some future directions. We need to improve delineation of breeding zones, incorporating climate, site factors, and pest problem areas. We should be avoiding monoculture and off-site planting. We may be selecting for too many traits. Second-generation breeding and selection techniques and progeny-test designs could be improved. Wild pollen contamination in seed orchards is a problem that needs attention. We must learn how to increase genetic gains as plateaus are attained, how to perserve germplasm, and how to breed minor species with minimum effort.

Additional keywords: Tree breeding, forest tree improvement.

My assignment is to take a broad look at past forest genetics research in the South and discuss problems needing emphasis. Aside from a few early special breeding programs, forest genetics research and tree improvement work began in earnest in the South about 1950. Accomplishments have been spectacular. Admittedly, this success was partly due to the strong demand for better seed by forest managers in the South. But it has also been due to the remarkably close cooperation and support of federal, state, and private agencies. Tree improvement programs in other regions have followed the southern mold, but never quite equaled it. Most of the research was oriented to solve practical genetics problems as they were encountered by the various tree improvement programs. These programs also stimulated research in related fields, especially entomology and physiology.

Dorman's recent book (1976) covers our achievements very well and I shall not elaborate on them. Rather, I shall point out some of the deficiencies and needs in our forest genetics research and take a brief look into the future. Topics are discussed in the sequence of major activities involved in tree breeding.

DELINEATION OF BREEDING ZONES

Delineation of breeding or planting zones is usually the first step in a breeding program. The breeder defines the areas and/or sites for which separate superior strains of trees are to be developed. Hopefully, each strain will perform well within all parts of the zone for which it was developed. But many mistakes in size and configuration are to be expected. The continuing refinements of the designated zones should be a normal ongoing part of forest genetics research and tree improvement work.

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[1] Retired, formerly Chief Plant Geneticist, Southeastern Forest Experiment Station, Forest Service, USDA, Olustee, FL 32072

Establishment of breeding zones for our southern species has been rather haphazard. This was largely due to the multiplicity of organizations involved in tree improvement and to their varied and often overlapping forest land holdings. Some organizations having widespread holdings have delineated breeding zones for their own purposes. But because of the lack of needed information they were to some extent delineated arbitrarily and partly on the basis of political boundaries. Other organizations, having limited land holdings, felt no need for delineating breeding zones and this was often justified. But now that much experimental information is available, we can try to rectify this situation. Soundly-based breeding zones would almost certainly increase genetic gains, decrease costs, and help eliminate duplication of effort in the future.

The best information for delineation of zones comes from seed source studies and from analyses of climate and other environmental factors. In the South many seed source studies have been established for most of our commercially important pines, and some climatic studies have been made. It would be very desirable for researchers to analyze all old and new data for each species as a whole, to reconsider breeding zones, and to make recommendations for further tests. In most cases, only local tests may be needed because the broad patterns over species ranges have already been established. In some situations we are using non-native seed (such as the well-known Livingston Parish loblolly pine), and long-term studies may be required.

Some of our commercially important hardwoods and pines still need study. In planning new seed source studies, I recommend emphasis on local tests. The whole species range should first be divided into relatively broad zones, based on climatic and site factors. The size and configuration of such zones would vary greatly by species but a typical zone might encompass 10 to 20 counties.

Then seed should be collected from various portions of each zone and planted at different locations and sites within the zone. This approach will provide the most desirable data -- data on the magnitude of seed source x planting site interaction within each preliminary zone. With this information any need for subdivision of zones can be determined. To get a broad picture of variation over the species' range, some seedlots (possibly bulked from adjacent collections) could be planted at several locations on key sites.

Any seed source studies that are needed will have to be established very soon because the increasing number of plantations will soon prevent installation of reliable tests. Native trees will often be pollinated by trees in nearby non-native plantations. Where serious diseases or pests occur, the degree of hazard should be surveyed and mapped, as was recently done for fusiform rust damage. Such maps are very useful in delineating breeding zones.

CHOICE OF SPECIES AND TRAITS

Many people feel that we have concentrated too much on slash and loblolly pines. These are sometimes planted where they do not grow as well as other species that are better adapted to the site. Research on longleaf pine and other species should be encouraged to alleviate this problem. Going further, we should consider the possible advantages of growing mixed stands, especially where species grow naturally in mixture with others. Establishment of many small mixed-species plantations would be desirable to learn of the problems that might be involved.

I believe we tend to select for too many traits. Studies designed to determine which can be eliminated would be in order. Intentional or unintentional selection for heavy flowering, for example, might be eliminated. On the other hand, I believe that in view of impending shortages of oil and other energy sources, we should consider more research with high-density, short-rotation plantations as a source of energy and chemicals. Likewise, breeding of Eucalypts and other hardwood species for high oil content may be in order.

BREEDING STRATEGIES

In recent years forest geneticists have developed a number of advanced-generation breeding strategies. The more sophisticated ones usually entail 1) controlled breeding of original selections made in the wild, 2) establishment of base populations from the progeny, 3) selection of the best individuals to establish new seed orchards, and 4) roguing of previous-generation orchards on the basis of progeny performance. Here are some problems needing study.

In some programs, original selections from widely separated regions are incorporated into a single strain. The goal is to develop a broad gene base for broad adaptability (Zobel, 1974), but I believe that we should be cautious in this crossing. Genetic gains are reduced in trying to develop strains that will be suitable over wide areas and over a variety of sites. A broad genetic base can be maintained, even within a relatively small breeding zone, by insuring that selections come from various stands within the zone and by avoiding excessive inbreeding in subsequent generations.

The common practice of establishing dual-purpose base populations needs further study. For progeny testing, large plots are preferable, while for selection of trees for new orchards, small plots may be more efficient (Stonecypher and Arbez, 1976). In progeny tests, keeping individual tree ancestry is not necessary and wind-pollinated (or polycross) progeny are sufficient. Perhaps separate plantings would be in order.

Highly intensive and sophisticated breeding approaches may not be justified for our minor species. Later in this paper I propose a simple procedure which will meet other objectives as well.

Techniques for vegetative propagation of superior trees on a commercial scale will likely become available for at least some species. We should now begin to think about how this capability might affect our breeding strategies.

SELECTION TECHNIQUES

Techniques for selecting superior trees were relatively simple in the first generation. Selection in subsequent generations is complicated by the presence of known relatives and other factors. Immediate research is needed on several problems.

Selection techniques should take the following factors into account simultaneously: (1) individual tree performance for each trait of interest, (2) performance of known relatives, (3) heritabilities and economic value of each trait and correlations between traits and (4) degree of juvenile-mature correlations for traits that are selected prior to maturity. Research on this problem in France (Arbez et al. 1974; Baradat, 1976) should be examined for possible application in our work.

Many of our progeny tests show pronounced microsite variation in small patches or fluctuating gradients (Figure 1). Randomized blocks account for little of this type of variation. Techniques or better designs are needed for testing significance of family differences in such situations, as proposed by Wright (1978) and Swindel and Squillace[2/] (In press). Likewise, techniques are needed to account for such variation when selecting and evaluating individual trees within families. One possibility is to compare statistically each individual against its immediate neighbors.

Correlations between some traits are still not clear. For example, the correlation between growth rate and survival (adaptability) has received little attention because of the difficulty of studying this in the first generation of selection. However, now that we have progeny tests established this can be studied, using family performance. Also, we are still not clear about relationships of growth rates to fusiform rust resistance and flower production. Methods of expressing some traits can cause false correlations and these should be examined. For example, expressing wood characteristics on a dry weight basis can cause false correlations with wood density and even affect heritability (Franklin and Squillace, 1974).

The efficacy of including relatives in second generation orchards needs study. Inclusion of relatives increases the permissible selection intensity (and hence genetic gain) but results in a loss due to inbreeding depression (Squillace, 1973; Lindgren and Gregorius, 1976). We need to improve our esti-

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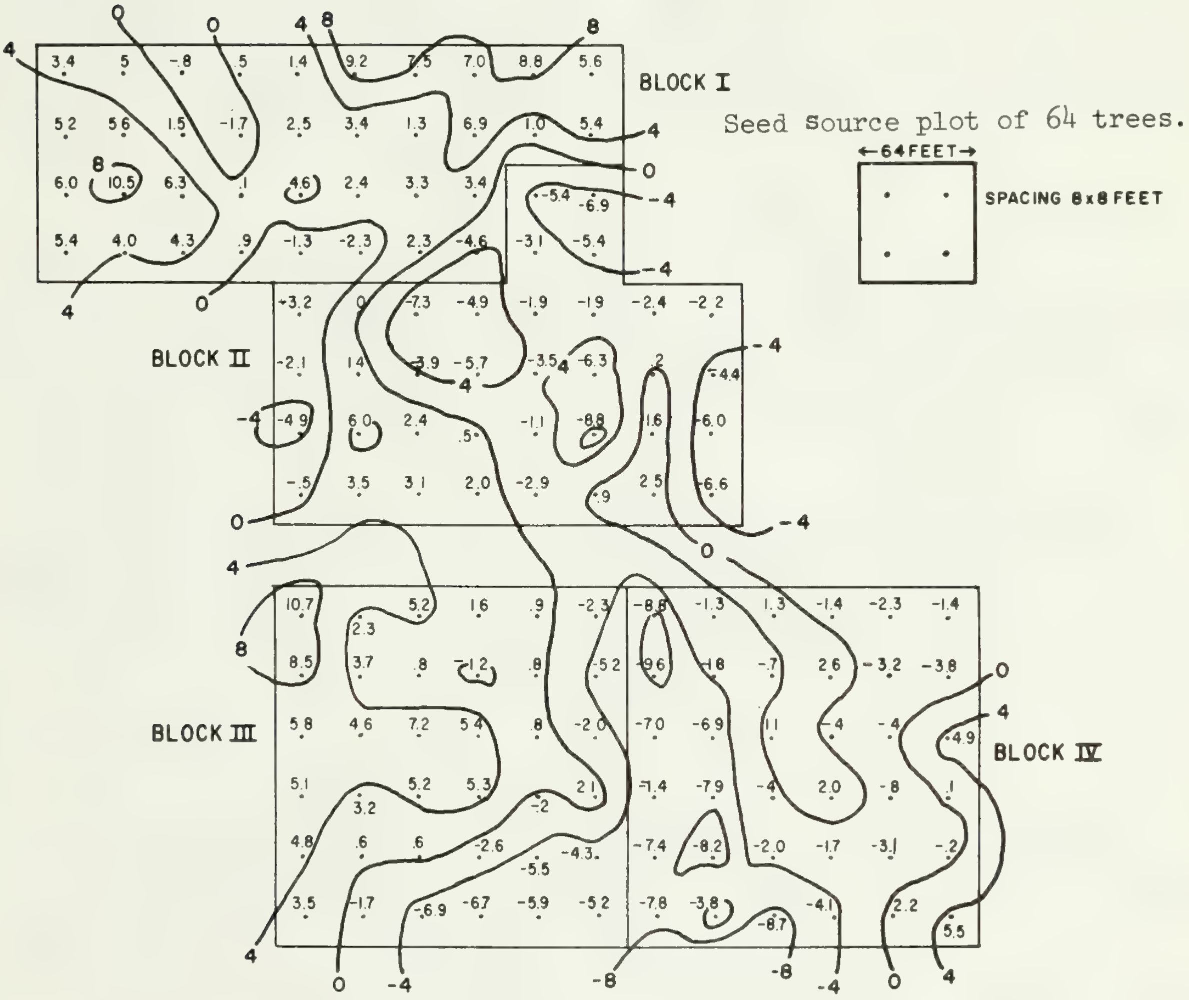
[2/] Manuscript entitled "A test for treatment effects in field experiments having severe microsite variation", by B. G. Swindel and A. E. Squillace.

Figure 1.-- Microsite variation in tree height in a loblolly pine seed source plantation at Olustee, FL at age 10 years. Value at each point is 1/4-plot mean expressed as deviation from overall seed source mean.



mates of the extent of inbreeding depression for various traits, and to determine how much relatedness can be permitted. If it is to be excluded entirely, then perhaps single-pair mating schemes (Libby 1973) for establishing base populations should be used in preference to those that produce many related families.

MATING DESIGNS

Trees are usually mated either to determine the breeding value of selections for use in seed orchards or to develop advanced-generation base populations. Among the many designs available some are most suitable for one and some for the other of the purposes noted (van Buijtenen, 1976). However, we urgently need good experimental data to determine which designs are the most suitable, both from an economic and a statistical viewpoint.

PROGENY TEST TECHNIQUES

I often have qualms about our progeny test techniques. This phase of tree improvement is very costly, especially when it involves tree breeding and periodic measurement of traits. Perhaps wind pollinated seed or polycrossing should be used more frequently (Kraus 1971; Snyder and Namkoong, 1978). More information on juvenile-mature correlations is needed. Curves of trait performance over time would be helpful to determine the best time to measure progeny tests.

Franklin[3] recently showed that genetic and environmental variances of some traits change with age, following definite patterns possibly associated with changing degree of competition. Such effects could have a strong bearing on test designs and on when to measure traits. The matter should be studied further, especially to see if progeny grown at close spacings and under favorable conditions will provide reliable estimates of genetic and environmental variances.

PROPAGATING SUPERIOR STRAINS FOR COMMERCIAL USE

Several problems associated with seed orchards deserve quick attention. Recent work suggests that wild pollen contamination may be high in some situations (Squillace, 1967; Hadders, 1973; Squillace and Long[4]). More study is needed on this problem and on methods of alleviating it. Techniques, using monoterpenes or isoenzymes as gene markers, are available for studying contamination. Some work is underway to determine advisability of moving seed orchards southward, mainly to increase seed yields but to also reduce contamination. This type of research should be encouraged.

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[3] Manuscript entitled "Model relating levels of genetic variance to stand development of four North American conifers", by E. C. Franklin, submitted to Silvae Genetica.

[4] Manuscript entitled, "Proportion of pollen from non-orchard sources", by A. E. Squillace and Ernest M. Long.

Seedling seed orchards seem to be gaining popularity. Planting designs and thinning procedures should be worked out to minimize inbreeding and maximize gains (Goddard and Brown, 1961; Rockwood and Kok, 1977).

Mass pollination techniques offer possibilities for increasing seed yields and genetic gains (Denison and Franklin, 1975). Research along this line should be helpful.

Recent work suggests that yield of selfed seedlings in slash pine seed orchards is probably no greater than in natural stands (Kraus, 1975). We need similar information on other important species.

The planting of vegetative propagules seems certain to become popular. We should be thinking about how best to utilize propagules in planting. For example, would interplanting of seedlings be desirable to stretch the limited supply of vegetative propagules?

ESTIMATING GENETIC GAINS

Many of our estimates of genetic gains are based on small plots in progeny tests in which competition effects cause misleading results. More study is needed on competition effects and data are needed on yield per unit area rather than per tree.

Estimates of genetic gain are usually based on heritability. Nanson (1976) recently pointed out that the heritability concept suffers from many limitations in forest tree breeding and that it should be replaced by some measure of correlation. Although his proposal seems good in theory, some aspects of it need to be checked by experiments.

PRESERVATION OF GERM PLASM

Many people fear that in the process of breeding and extensively planting superior trees, we may lose germ plasm which although not presently desirable, may be needed in the future as environments or man's needs change. Storage of seed has been suggested as a means of preservation . However, such a technique would eventually require planting followed by recollection and storage. This procedure would have to be followed for collections made from various parts of the range of each species. Also, in the replantings we would have to avoid contamination of pollen from other sources.

In view of these problems, a more practical procedure might be to establish a number of small natural areas, over the entire range of each species. The feasibility and techniques for doing this need study. Germ plasm could also be preserved in seed production areas in which modest genetic gains could also be made. This possibility is discussed in the next section of this report.

A LOOK INTO THE FUTURE

It is very likely that eventually we will run into a plateau of superiority for the traits we are trying to improve -- maybe sooner than we think. I am confident that we can continue to increase growth rate, for example, for several generations, but the gains are likely to decrease with time. In addition to simply running out of genetic variation in growth rate there is very likely a physiological limitation on how fast trees can grow and still be resistant to the rigors of environment. Too, there is the possibility that environments may change. The fusiform rust pathogen, for example, might mutate and become capable at attacking resistant strains of pines. Finally there is a likelihood that human needs, such as products desired from trees, may change.

How are we going to continue to make improvements in the face of these probable events? One possibility is to decrease the size and nature of our breeding zones greatly and develop separate strains for each zone. This approach would not only increase genetic gains but also maintain a large gene pool -- trees bred for different sites or different parts of the species' range would likely be genetically different. This admittedly could also be very costly, and would also eventually encounter thresholds of gains.

In a recent study of the problem of depleting genetic resources, Namkoong (1974) noted that we can attempt to achieve an optimum balance between immediate exploitation (large early genetic gains) and a slower utilization of such resources providing for future gains. This proposal can well be studied further.

What are we going to do about minor species, for which intensive and sophisticated breeding procedures cannot be justified? Here is a suggestion that may be considered for minor species and possibly also for special situations.

1. Divide the entire species range into many planting zones (say from 20 to 40), using the best knowledge available on climate, site factors, and pest problems.

2. Pick at least two phenotypically good, young stands (or good native plantations if available) in each zone. Thin them, using the best selection techniques available, for conversion into seed production areas.

3. Collect seeds from these areas and plant them only in their respective planting zones.

4. As soon as these plantings reach fruiting age, establish new seed production areas for each zone.

5. Collect seeds from the new seed production areas as soon as possible, dropping the old ones.

6. Repeat the process indefinitely, or initiate sophisticated breeding procedures when and if justified.

Note that under this procedure, although the breeder has imposed some degree of artificial selection, natural selection will also occur for adaptability and resistance to adverse environmental factors of the breeding zone. If the environmental factors change with time, so will the population of survivors change. Further, I doubt that the breeder would have to face inbreeding problems, the problem of deterioration of some traits at the expense of others, or genotype-environment interactions. Finally, I believe that, although some degree of artificial selection is imposed, a wide genetic base will be maintained by preserving stands in many widely separated areas.

This proposal is not really new; the seed production area has been frequently used in the past. The only added features are that the whole species range is systematically covered and that the process of mass selection is continued. The procedure could probably also be used in special situations such as in high fusiform rust hazard areas, where genetic differences in the pathogen may occur over the species range or change with time.

Although forest genetics researchers of the South have made remarkable achievements in providing the bases for developing superior trees, there is room for improvement. We could have done a better job in some areas, such as in studies of geographic variation, delineation and refinement of breeding zones, and techniques for comprehensive preservation of germ plasm. Such studies require consideration of the entire range of each species and therefore need highly centralized planning and coordination to avoid duplication and to obtain maximum information. Deficiencies in this regard were partly due to the mixed ownership patterns of forest lands and the multiplicity of research organizations. This situation has been considerably alleviated by the coordinating efforts of such organizations as the Southern Forest Tree Improvement Committee and the Regional Tree Improvement Project S-23. Both should be strongly supported.

Some of the deficiencies in our work were due simply to the newness of our endeavor -- we sometimes were groping in the dark. Also, new problems keep cropping up, as might be expected in any endeavor of this type. But with continued excellent support and cooperation as obtained in the past, these new problems can be solved.

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GENETIC VARIATION IN MISSISSIPPI SWEETGUM

O. O. Wells, G. L. Switzer, and W. L. Nance[1]

Abstract.--Seed was collected from 650 sweetgum trees throughout Mississippi and southeastern Louisiana during 1962, 1963, and 1964. Progeny plantings were established in south Mississippi, central Mississippi, and southwest Tennessee. After 10 years, well defined latitudinal and longitudinal patterns of variation in height growth were evident among the half-sib progenies. Progenies from southeastern Mississippi excelled in all three plantings, but the zone of fastest growth for the northernmost planting was farther northwest than for the other plantings. Progenies from near the Mississippi-Alabama border grew faster than those from the floodplain of the Mississippi River or the loessal hills that border the floodplain to the east.

Additional keywords: Liquidambar, genecology.

INTRODUCTION

Research on geographic variability and population structure is basic to forest tree improvement programs. To be most efficient, programs should take advantage of all levels of genetic variation--geographic, stand to stand, and individual tree. Substantial tests of geographic variability with sweetgum (*Liquidambar styraciflua* L.) have been established by the Western Gulf Tree Improvement Cooperative (Texas Forest Service 1975), the North Carolina State Tree Improvement Cooperative (Sprague and Weir 1973), and the Southern Forest Experiment Station. These tests are expected to provide guidelines for movement of seeds from one area to another in the near future.

The provenance-progeny test reported here was begun in 1962 to characterize genetic variability throughout Mississippi, in adjacent parts of Alabama, and in the Florida Parishes of Louisiana. We sampled the population intensively enough to compare variability associated with latitude, among stands, and from tree-to-tree. Besides characterizing genetic variation, the tests can provide outstanding material to be used in improvement programs in and near Mississippi. This report gives results after 10 years in the field.

METHODS

The study area is bounded on the west by the Mississippi River drainage and on the east by the drainage of the Tombigbee and Alabama Rivers (fig. 1). Seed collection locations (sources) were planned by dividing the area into 20 latitudinal transects, 15 minutes of latitude apart, and mapping a collection point every 30 miles along the transects. Collections were made within 10 miles of these points. Fruit was collected in 1962, 1963, and 1964 from five trees in each of a total of 138 sources. Criteria for selecting parent trees were undemanding. The first five fruiting trees of any age to be sighted from the road within a specified location were chosen if they were between 200 feet and 1/4th mile apart and were within 100 feet of other fruiting sweetgum.

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[1] U.S. Forest Service, Gulfport, MS and Mississippi State University, Starkville, MS. International Paper Co. and the University of Tennessee made land available for the experiment.

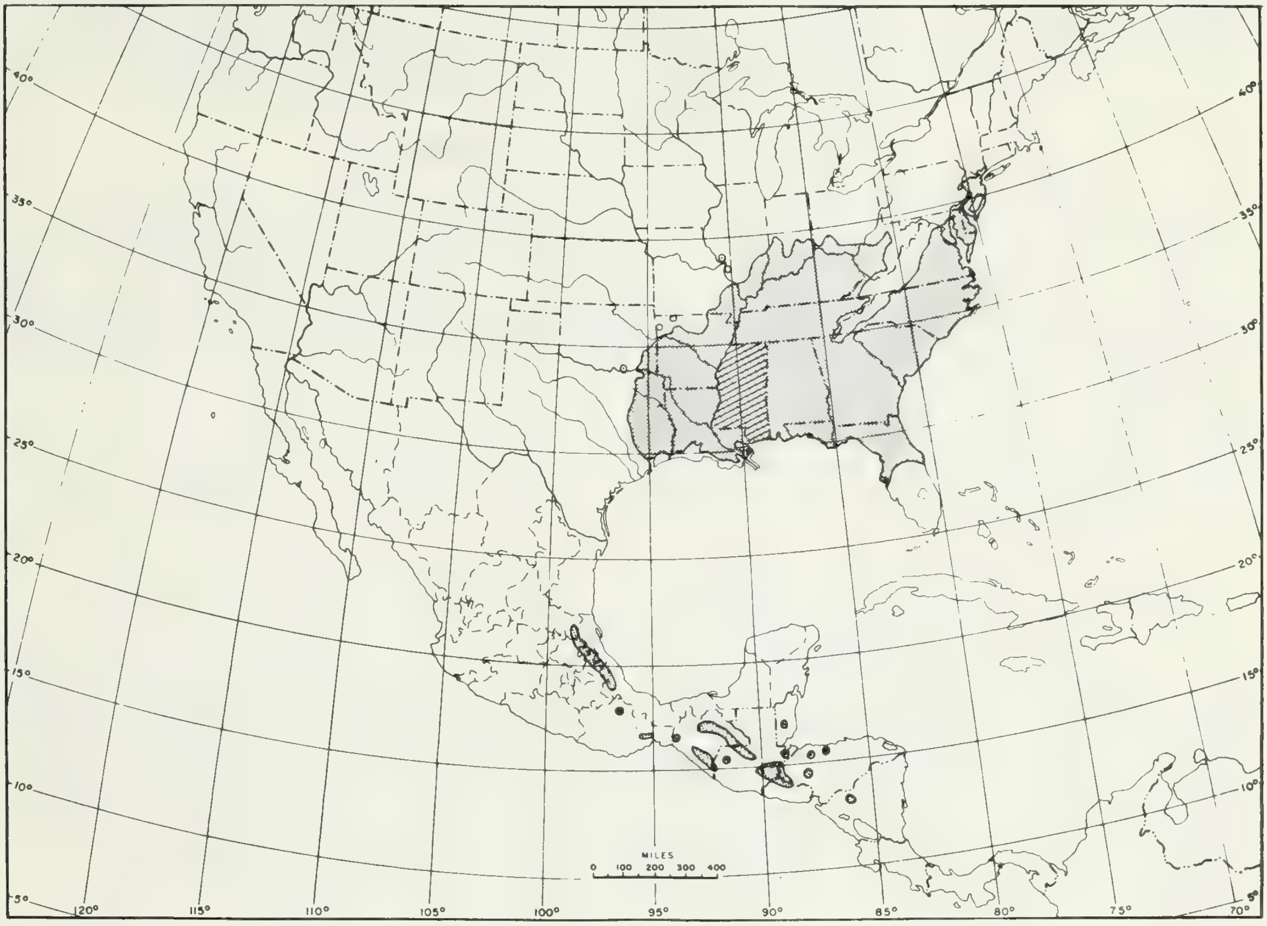

Figure 1.--The range of sweetgum and the present study area

During 1965, planting stock was grown in a three replicate design near Gulfport, Mississippi. The seedlings were planted during winter 1965-66 in three locations: near Pearlington in south Mississippi, near Mississippi State University in central Mississippi, and on the Ames Plantation, University of Tennessee in southwestern Tennessee. Stock at each location was from one nursery replication. The field design was a 10-replicate, compact family block (Panse and Sukhatme 1965) with two-tree family plots and 10-tree source plots. (As used here, family means the wind-pollinated progeny of one tree.) This design grouped the five, two-tree family plots that represented a source (the five parent trees in each collection area) rather than distributing the family plots at random over each replication. Spacing was 8 by 8 feet and each replication was about 2.0 acres. A border row was used to offset edge effects.

The central Mississippi and Tennessee planting sites were bottomland old fields that had been abandoned for many years. The alluvial soil was covered mostly with grass. The southern Mississippi planting was on recently cleared forest land (loblolly pine and mixed hardwoods, including sweetgum) on a low sandy ridge adjacent to marshland along the north coast of Lake Borgne. The topsoil was thin, and much of it was lost during site preparation.

Grasses were partially controlled in all plantings by mowing and application of herbicide around each tree. Growth was slow in the early years in all plantings (trees were less than 5 feet tall after 4 years), but generally rapid thereafter. Because of poor growth, three blocks were discarded in the northern and southern plantings and two in the central planting (Table 1). Survival averaged 83.6 percent in the remaining, usable blocks. After 10 years, trees averaged 8.2, 14.0, and 14.1 feet tall in the southern, central, and northern plantings.

Table 1.--Characteristics of the experiment after 10 years

			Sources having				
Planting	Blocks	Sources	5 families	4 families	3 families	Usable family plots	Missing family plots
			number				percent
Pearlington, MS (southern)	7	138	125	10	3	4316	12.0
Miss. State University(central)	8	136	125	7	4	4063	23.6
Ames Plantation TN (northern)	7	133	118	9	6	3891	13.7

MEASUREMENTS AND ANALYSIS

This report describes the genetic variation in the trait of greatest economic importance--height at 10 years. ANOVA was used to determine if there were differences in height among families in each of the 138 sources in each of the 3 plantings. Degrees of freedom for a typical analysis were: blocks = 6, families = 4, error = 24. The experimental unit was the mean of the 2-tree family plots. Values were calculated for missing plots; augmented means were used thereafter, and adjustments were made to the treatment sums of squares and degrees of freedom for error (Yates 1933).

Further ANOVA were used for testing for differences among sources and families over all plantings as follows:

Source of Variation	Degrees of Freedom	Mean Square
Plantings	2	60086.9*
(a) Blocks within plantings	19	10158.7
Sources	130	137.4*
Sources x plantings	260	78.7
(b) Sources x blocks within plantings	2302	68.9
Families within sources	492	23.7*
Families within sources x plantings	984	11.2
(c) Families within sources x blocks within plantings	7547	12.0

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*Significant differences at the 0.05 level of significance

Statistical analyses were used primarily to detect differences among family and source means. More sophisticated calculations, particularly those based on expected mean squares, such as estimation of genetic variances and heritability, were not considered feasible because of the many missing values, the considerable environmentally induced variation within blocks, and other imbalances in the design. Although the statistical analysis is only an approximation, it still is a powerful test because of the large number of families tested. This design gave a more detailed delineation of the geographic variation pattern and a larger genetic base for future breeding work than would have been obtained from a smaller, more precise test of fewer families.

RESULTS AND CONCLUSIONS

Variation among sources--After 10 years, a well defined latitudinal and longitudinal pattern in height growth was evident (figures 2, 3, 4). Sources from southeastern Mississippi excelled in all three plantings, but in the northern planting fastest growth was centered farther to the northwest than in the other plantings. The southeastern sources generally are well adapted (at least for 10 years) to climates up to about 250 miles north of their point of origin.

The latitudinal variation pattern seems to be a straightforward selection response to climate. Populations that have developed in mild climates tend to grow faster than those from harsher climates if the comparison is made in a relatively mild climate.

The reason for the longitudinal variation pattern is more cryptic. At any given latitude, sources from the western part of the study area (near the Mississippi River) grew more slowly than those from near the Mississippi-Alabama border. The contrast is especially distinct in the southern Mississippi planting between sources from coastal Mississippi and southeastern Louisiana. The slow growth of sources from the floodplain of the Mississippi River and the loessal hills along the eastern border of the floodplain is distinct in all three plantings sites.

This difference cannot be explained by climate, but it could be related to soil type. The slow-growing trees came from sites far more fertile than did the fast-growing ones, and selection for fast growth is generally greatest on optimum sites (Squillace and Kraus 1959). It is possible that sweetgum from the fertile soils of the alluvial plain of the Mississippi River does not grow to its potential on less productive sites such as those in the present study. Some evidence of edaphic ecotypes in sweetgum from different soil types in the Mississippi Delta has been found[1], so there is support for this hypothesis.

Another plausible hypothesis is that the Mississippi and Ohio Rivers transport seed from near the northern extremity of the sweetgum range in Ohio, Illinois, and Indiana (fig. 1) and provide a constant flow of genes for slow growth into the population growing in the floodplain of the Mississippi River. Genes for slow growth might drift eastward away from the River until their effect is overcome by sweetgum from southeastern Mississippi, which has evolved in place, the tendency

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[1] Personal communication from D. T. Cooper of the Southern Forest Experiment Station, Stoneville, Mississippi.

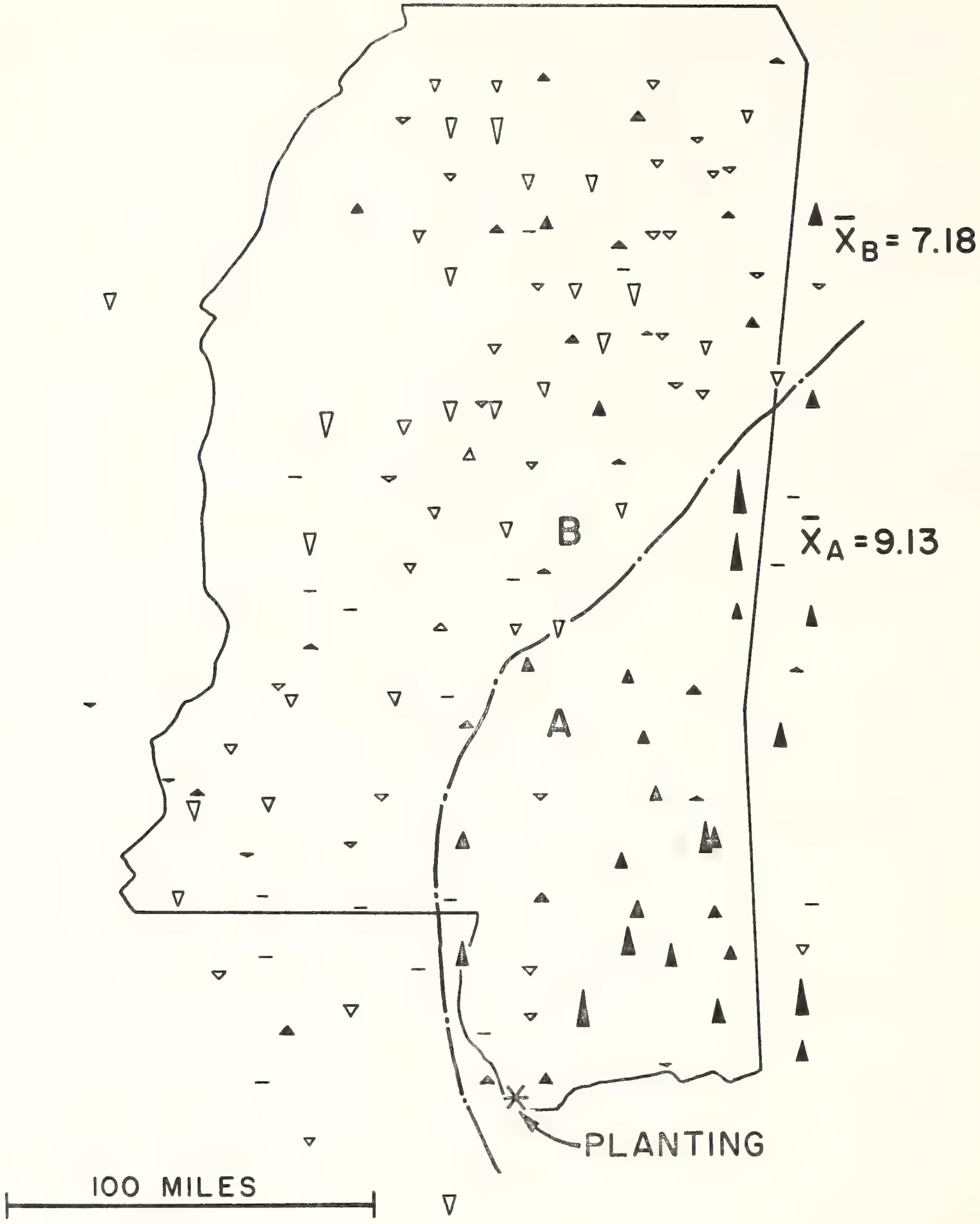

Figure 2.--Average 10-year height of the five families from each source growing in the southern planting. ▲ = source above the planting mean, ▽ = source below the planting mean. Height of the triangles are proportional to the source mean height. Average height of the sources inside (A) and outside (B) the optimum seed collection zone is shown.

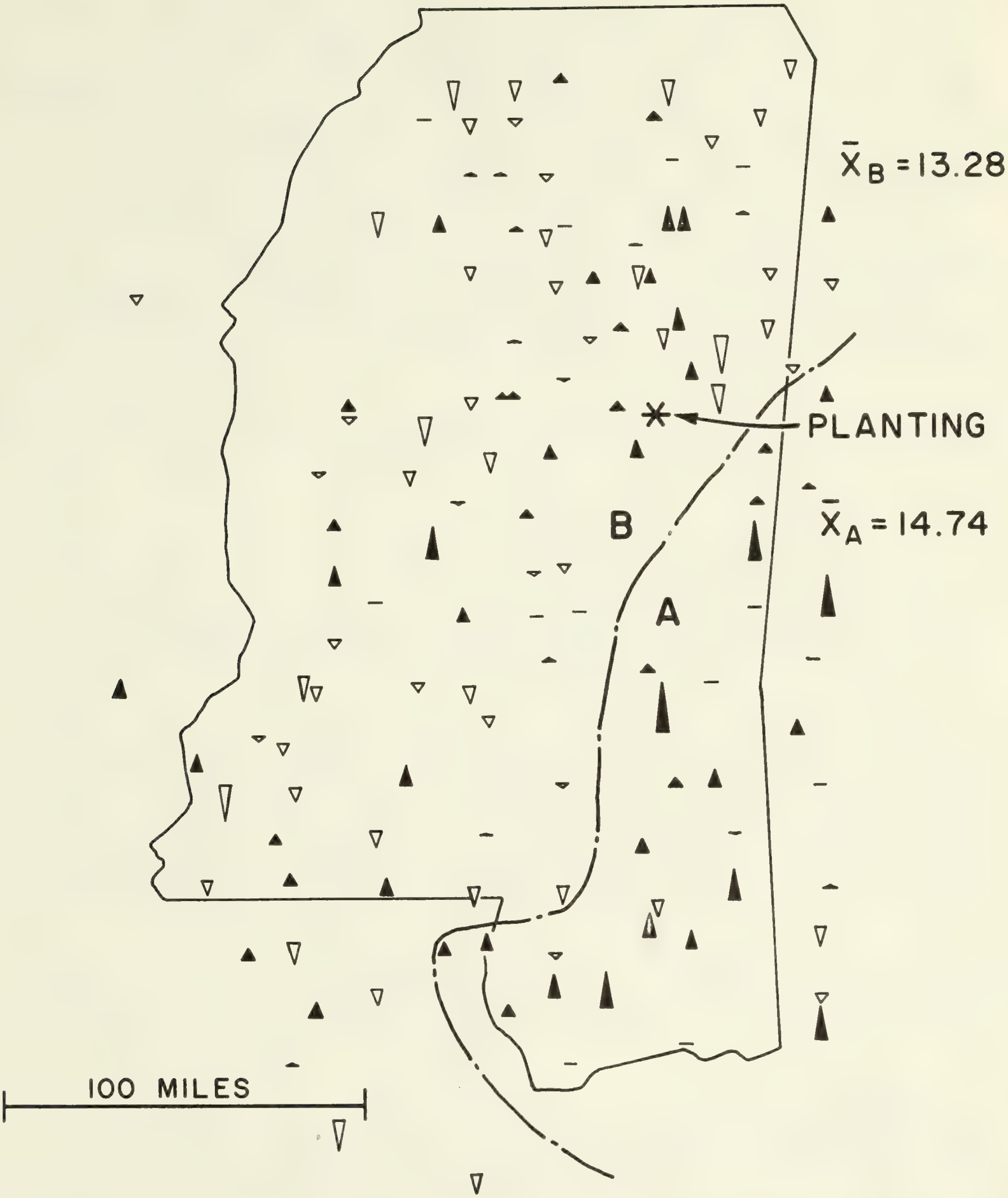

Figure 3.--Average 10-year height of the five families from each source growing in the central planting. ▲ = source above the planting mean, ▽ = source below the planting mean. Height of the triangles are proportional to the source mean height. Average height of the sources inside (A) and outside (B) the optimum seed collection zone is shown.

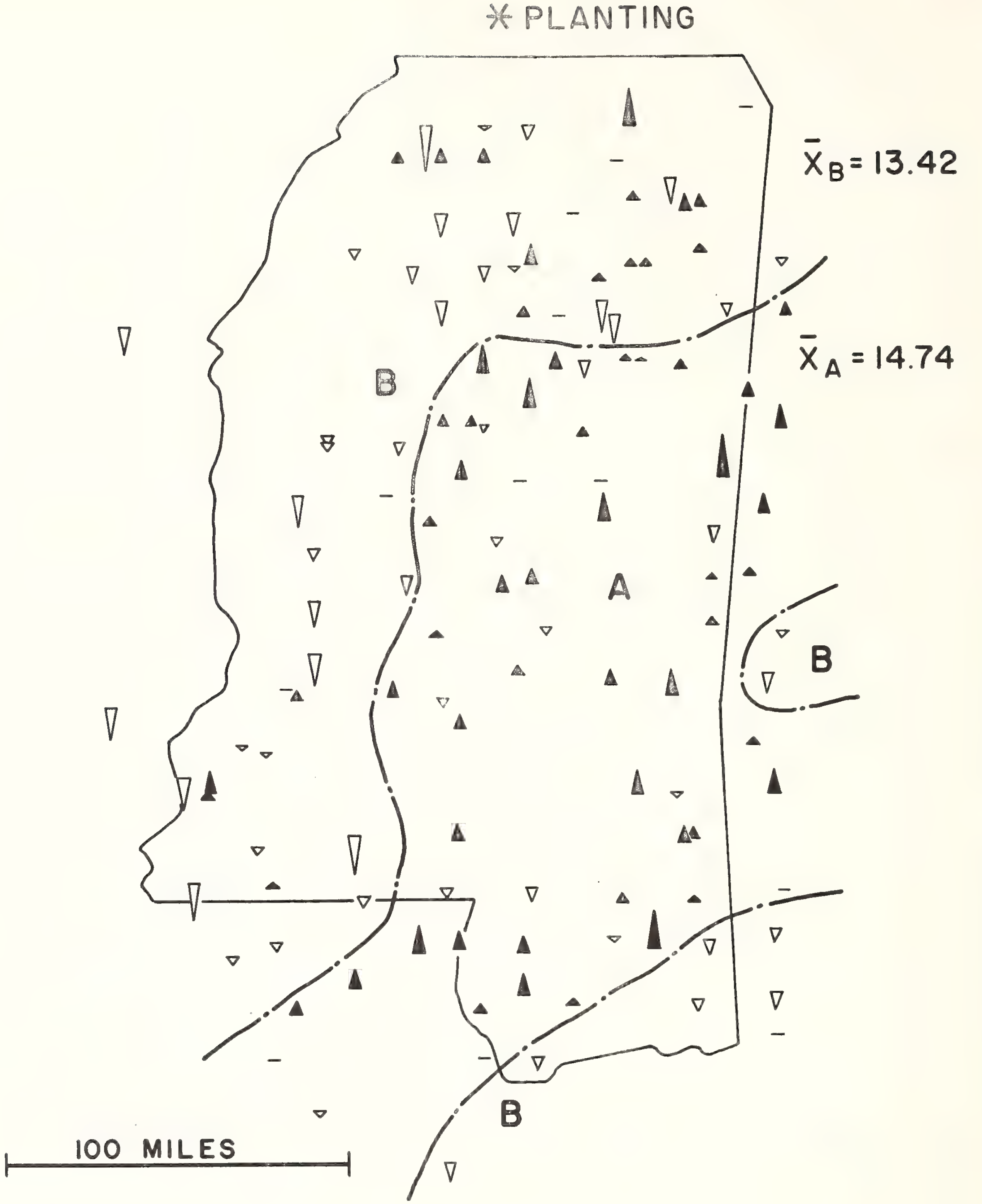

Figure 4.--Average 10-year height of the five families from each source growing in the northern planting. ▲ = source above the planting mean, ▽ = source below the planting mean. Height of the triangles are proportional to the source mean height. Average height of the sources inside (A) and outside (B) the optimum seed collection zone is shown.

for faster growth. Unlike the Mississippi and Ohio Rivers, the lesser drainages in the study area (Tombigbee, Pearl, Pascagoula Rivers) have their headwaters at least 500 miles south of the sweetgum populations in Ohio, Illinois, and Indiana, and would not have such slow-growing germ plasm to transport downstream.

Within source variation--On the average, there was a demonstrable amount of genetic variation among the families within a source and as indicated by the lack of significance for family within source x location interaction, the amount of this variation does not change significantly from planting to planting. The F value of 1.97 for family within source is small and statistical significance seems to be the result of a small biological effect and many degrees of freedom (492 over 7547). Another test of the within-source effect is the ANOVA of each source where the five families were tested in seven or eight blocks at each planting location. On this basis, significant differences in height among families occur in about 9.8% of the sources at any one planting location, as the following tabulation shows:

Planting	Sources	Sources with significant differences among the families within	
	(number)	(number)	(percent)
Southern	138	10	7.2
Central	136	19	14.0
Northern	144	12	8.3
Total	418	41	$\bar{x}$ = 9.8

Family differences were sizeable in the cases where significance was attained. The average difference between the best family in a source and the mean of the families in that source was 2.7 feet, an advantage of 24% over the source mean (Table 2).

The sampling and planting design of this experiment was nested, so G x E interaction for families refers only to the amount of variation within each source and indicates nothing about whether the family means change rank from planting to planting. We looked at rank changes by inspection of the family means in those sources where genetic differences existed (Table 3). In about half of the 38 sources where there were differences in height, the family or families primarily responsible for the within source difference performed about the same in at least one other planting.

Thus, demonstrable differences in growth rate occur in about 10% of the sources tested and the fast-growing families exhibit fairly strong G x E stability. This is solid evidence that a breeding program for enhanced vigor in sweetgum would be biologically feasible.

APPLICATION

The best trees growing in the test plantation of the study will be used for a breeding program. The objective of this program is to produce improved strains for Mississippi, adjacent parts of Alabama and Tennessee, and the Florida Parishes of Louisiana, that is, the area covered by the present study. These improved strains are likely to be adapted to other parts of the southeastern U.S. as well. Results from several other sweetgum provenance tests underway in the South should soon be available for developing guidelines for sweetgum seed movement.

These results should also serve as a general guide to sweetgum improvement programs outside of the present study area. It is likely that the latitudinal

Table 2. — *Family and source means for sources having significant between-family differences (feet).*

Southern Planting				Central Planting				Northern Planting			
Source	Family	$\bar{x}_f$	$\bar{x}_s$	Source	Family	$\bar{x}_f$	$\bar{x}_s$	Source	Family	$\bar{x}_f$	$\bar{x}_s$
047	1	10.5		031	2	15.7		033	1	21.7	
	4	9.3			3	14.4			2	19.5	
	5	6.7	7.6		1	12.9	13.0		3	15.4	16.2
	3	5.9			4	12.4			5	12.9	
	2	5.6			5	9.5			4	11.5	
145	4	8.3		041	5	14.5		022	3	15.7	
	3	7.6			3	14.5			2	15.3	
	1	7.5	6.8		1	13.2	11.9		1	13.6	13.1
	5	5.4			4	8.9			5	10.9	
	2	5.2			2	8.4			4	10.0	
243	1	9.1		125	2	13.6		035	2	21.9	
	2	7.0			1	13.0			3	18.1	
	4	5.8	6.4		4	11.9	12.1		1	17.1	16.5
	5	5.6			3	11.9			4	13.8	
	3	4.5			5	10.3			5	11.5	
321	1	11.6		126	3	16.6					
	2	11.1			2	15.9		212	1	19.7	
	3	9.7	9.4		1	14.4	14.5		2	18.9	
	5	7.5			5	13.5			4	16.8	17.1
	4	7.2			4	12.1			3	16.7	
									5	13.4	
331	1	10.3		142	5	23.2					
	2	9.0			4	21.7					
	4	8.1	7.9		1	17.3	18.8	412	1	17.8	
	3	6.8			2	16.1			3	16.6	
	5	5.5			3	15.8			2	16.6	15.0
									4	12.5	
346	3	9.8		214	1	15.9			5	11.3	
	4	9.0			5	15.3					
	2	8.4	7.3		3	14.1	14.1	414	3	18.4	
	1	5.2			2	13.1			2	16.0	
	5	4.0			4	11.9			5	14.6	14.9
									1	14.3	
414	3	10.6		224	2	16.1			4	11.4	
	5	9.7			4	14.0					
	4	8.3	8.4		5	13.5	13.8	423	2	17.8	
	2	7.2			3	13.0			3	17.7	
	1	6.1			1	12.2			4	14.5	15.1
									5	13.2	
415	4	11.2		225	3	17.2			1	12.1	
	3	10.6			5	16.1					
	5	10.2	8.9		4	15.8	15.2	235	5	16.1	
	2	7.5			2	14.9			2	14.7	
	1	5.1			1	11.8			4	11.9	12.3
									1	10.4	
424	3	8.0		234	1	16.7			3	8.6	
	1	6.4			2	14.7					
	4	6.0	6.0		3	14.1	13.5	245	5	18.8	
	5	5.5			5	11.2			3	15.9	
	2	4.3			4	10.7			4	14.8	15.1
									1	13.7	
427	5	9.3		244	4	16.6			2	12.3	
	4	7.6			1	15.5					
	1	7.1	7.1		2	13.7	14.3	424	2	16.4	
	3	6.2			5	13.0			5	16.0	
	2	5.4			3	12.6			4	14.6	14.5
									3	14.4	
				312	2	18.1			1	10.9	
					1	16.3					
					3	15.1	15.3	425	5	15.2	
					4	13.9			3	12.2	
					5	13.0			4	12.2	11.7
									2	10.4	
				345	1	17.4			1	8.5	
					2	15.4					
					3	13.9	14.8	436	3	21.1	
					5	13.8			2	16.0	
					4	13.7			1	15.6	15.3
									4	13.5	
				431	2	13.9			5	10.2	
					1	12.7					
					5	12.1	12.1	444	5	15.9	
					3	10.9			1	15.6	
					4	10.7			4	14.3	13.9
									2	12.7	
				348	3	14.4			3	11.2	
					5	13.6					
					4	13.5	12.4	435	3	18.4	
					2	10.3			4	17.2	
					1	10.1			2	15.1	
									1	14.0	
				418	2	14.5			5	13.8	
					1	13.6					
					3	9.7	11.1				
					4	9.2					
					5	8.6					
				427	5	17.2					
					3	14.7					
					4	14.0	14.0				
					2	12.5					
					1	11.5					
				236	4	16.7					
					1	16.4					
					2	16.1	15.7				
					5	15.4					
					3	13.9					
				436	5	15.7					
					1	13.8					
					4	13.4	13.6				
					3	12.9					
					2	12.2					
				315	3	15.3					
					4	13.4					
					5	12.8	12.3				
					2	10.8					
					1	9.2					

Table 3. — *Family within source x planting site interaction for sources that had significant differences among the families within them at one planting or another. Instances of stable performance are underlined.*

Source	Planting 1/					
	Southern		Central		Northern	
	Family	Ht.	Family	Ht.	Family	Ht.
047	1	10.5	5	19.6	5	19.0
	4	9.3	4	17.5	2	14.8
	5	6.7	3	17.4	4	14.6
	3	5.9	1	16.3	1	13.8
	2	5.6	2	15.2	3	12.8
145	4	8.3	2	14.9	2	14.3
	3	7.6	3	14.4	1	14.0
	1	7.5	4	13.1	4	13.3
	5	5.4	1	12.3	3	12.5
	2	5.2			5	11.7
243	1	9.1	5	19.3	4	16.0
	2	7.0	3	18.0	1	15.8
	4	5.8	1	14.6	2	13.7
	5	5.6			5	13.6
	3	4.5				
321	1	11.6	5	21.5	1	16.2
	2	11.1	1	16.5	3	15.6
	3	9.7	3	16.3	2	14.9
	5	7.5	2	15.4	5	14.8
	4	7.2	4	14.5	4	13.9
331	1	10.3	1	17.8	1	13.1
	2	9.0	2	14.7	3	12.5
	4	8.1	3	14.3	2	12.0
	3	6.8	5	14.0	5	11.2
	5	5.5	4	13.2	4	9.7
346	3	9.8	2	18.4	4	13.1
	4	9.0	1	16.0	5	13.1
	2	8.4	4	15.2	3	12.3
	1	5.2	3	14.7	2	12.2
	5	4.0	5	12.1	1	11.9
414	3	10.6	4	15.0	3	18.4
	5	9.7	5	14.5	2	16.0
	4	8.3	2	14.4	5	14.6
	2	7.2	3	12.8	1	14.3
	1	6.1	1	12.2	4	11.4
415	4	11.2	4	15.8	2	18.0
	3	10.6	1	14.6	1	17.4
	5	10.2	3	13.5	5	16.3
	2	7.5	2	13.2	4	15.7
	1	5.1	5	11.9	3	14.2
424	3	8.0	2	12.7	2	16.4
	1	6.4	4	12.5	5	16.0
	4	6.0	3	12.1	4	14.5
	5	5.5	1	11.8	3	14.4
	2	4.3	5	10.6	1	10.9
427	5	9.3	5	17.2	3	13.0
	4	7.6	3	14.7	2	12.9
	1	7.1	4	14.1	5	11.9
	3	6.2	2	12.5	4	11.2
	2	5.4	1	11.5	1	10.6

Source	Plantings 2/					
	Northern		Southern		Central	
	Family	Ht.	Family	Ht.	Family	Ht.
033	1	21.7	3	9.2	1	14.9
	2	19.5	1	7.6	5	14.0
	3	15.4	5	7.2	4	13.6
	5	12.9	4	6.9	2	13.2
	4	11.5	2	6.8	3	12.7
022	3	15.7	1	10.4	2	14.8
	2	15.3	2	9.3	5	14.6
	1	13.6	5	8.2	4	14.6
	5	10.9	3	8.1	3	13.6
	4	10.0	4	7.4	1	11.6
035	2	21.9	5	8.2	1	17.6
	3	18.1	2	8.0	5	17.6
	1	17.1	1	8.0	4	17.1
	4	13.8	4	6.3	3	15.0
	5	11.5	3	6.1	2	13.8
412	1	17.8	1	11.4	2	15.9
	3	16.6	5	8.8	1	15.2
	2	16.6	3	7.6	3	14.8
	4	12.5	2	7.0	5	12.6
	5	11.3	4	6.6	4	11.1
414	3	18.4	3	10.6	4	15.0
	2	16.0	5	9.7	5	14.5
	5	14.6	4	8.3	2	14.4
	1	14.3	2	7.2	3	12.8
	4	11.4	1	6.1	1	12.2
423	2	17.8	3	8.2	1	15.0
	3	17.7	2	7.4	3	14.1
	4	14.5	4	7.2	4	13.8
	5	13.2	1	6.5	2	13.8
	1	12.1	5	5.6	5	11.7
235	5	16.1	4	8.3	3	18.1
	2	14.7	2	7.6	5	17.6
	4	11.9	3	6.8	2	17.4
	1	10.4	5	6.7	1	17.3
	3	8.6	1	5.3	4	15.5
245	5	18.8	3	10.2	5	14.2
	3	15.9	5	6.1	3	14.0
	4	14.8	4	6.0	4	13.6
	1	13.7	1	5.9	1	13.2
	2	12.3	2	5.5	2	12.8
425	5	15.2	4	7.9	4	15.8
	3	12.2	2	6.6	2	13.5
	4	12.2	3	6.4	3	12.9
	2	10.4	5	6.3	5	12.3
	1	8.5	1	4.2	1	11.3
435	3	18.4	5	7.4	4	13.9
	4	17.2	3	5.6	5	12.4
	2	15.1	4	5.5	3	11.7
	1	14.0	1	4.9	1	11.6
	5	13.8	2	4.7	2	11.5
436	3	21.1	3	8.7	5	15.7
	2	16.0	2	7.5	1	13.8
	1	15.6	5	7.4	4	13.4
	4	13.5	1	6.8	3	12.9
	5	10.2	4	6.7	2	12.2
444	5	15.9	1	7.0	5	14.0
	1	15.6	2	6.8	2	12.2
	4	14.3	5	6.4	4	11.3
	2	12.7	3	6.3	3	11.2
	3	11.2	4	6.1	1	10.6
212	1	19.7	1	9.8	1	14.7
	2	18.9	4	9.8	4	14.6
	4	16.8	2	8.8	2	14.2
	3	16.7	5	8.6	3	13.9
	5	13.4	3	6.2	5	10.4
424	2	16.4	3	8.0	2	12.7
	5	16.0	1	6.4	4	12.5
	4	14.6	4	6.0	3	12.1
	3	14.4	5	5.5	1	11.8
	1	10.9	2	4.3	5	10.6

Source	Plantings 3/					
	Central		Southern		Northern	
	Family	Ht.	Family	Ht.	Family	Ht.
031	2	15.7	2	12.4	5	15.3
	3	14.4	3	11.3	1	13.0
	1	12.9	1	11.3	2	11.4
	4	12.4			3	11.3
	5	9.5			4	10.7
041	5	14.5	3	8.6	5	15.4
	3	14.5	5	7.6	3	13.5
	1	13.2	2	7.3	2	12.5
	4	8.9	1	7.3	4	12.2
	2	8.4	4	4.9	1	11.2
125	2	13.6	1	8.9	1	12.7
	1	13.0	3	7.7	3	12.0
	4	11.9	4	7.2	5	11.2
	3	11.9	5	7.0	2	9.0
	5	10.3	2	6.7	4	4.8
126	3	16.6	1	8.5	1	14.6
	2	15.9	2	8.5	5	14.6
	1	14.4	3	8.2	3	13.7
	5	13.5	4	7.3	2	12.9
	4	12.1	5	5.5	4	11.8
142	5	23.2	4	10.5	5	18.6
	4	21.7	5	9.6	4	17.9
	1	17.3	3	8.8	1	16.1
	2	16.1	2	8.7	2	13.2
	3	15.8	1	6.7	3	12.3
214	1	15.9	1	10.8	1	17.9
	5	15.3	2	9.8	2	16.9
	3	14.1	3	9.7	3	14.2
	2	13.1	4	7.9	5	13.5
	4	11.9	5	7.4	4	13.4
224	2	16.1	5	7.6	2	18.3
	4	14.0	4	7.4	5	17.5
	5	13.5	2	7.2	4	17.4
	3	13.0	3	6.6	3	17.0
	1	12.2	1	4.9	1	13.4
225	3	17.2	2	8.8	5	16.6
	5	16.1	3	8.7	4	16.0
	4	15.8	1	8.3	3	16.0
	2	14.9	5	8.3	2	15.5
	1	11.8	4	7.2	1	9.6
234	1	16.7	4	9.2	4	18.1
	2	14.7	5	7.8	3	17.4
	3	14.1	1	7.5	1	16.1
	5	11.2	2	7.4	2	14.5
	4	10.7	3	5.5	5	14.1
244	4	16.6	5	8.8	3	16.4
	1	15.5	3	6.6	4	14.3
	2	13.7	1	5.6	5	14.2
	5	13.0	2	5.4	2	11.1
	3	12.6	4	5.4	1	10.9
312	2	18.1	5	9.7	1	16.0
	1	16.3	1	7.9	2	15.8
	3	15.1	3	7.8	5	15.4
	4	13.9	2	7.7	4	13.1
	5	13.0	4	7.1	3	12.3
345	1	17.4	4	7.6	1	17.2
	2	15.4	3	7.3	4	14.4
	3	13.9	2	7.0	2	13.3
	5	13.8	1	6.6	3	13.2
	4	13.7	5	4.1	5	12.7

Source	Plantings 3/					
	Central		Southern		Northern	
	Family	Ht.	Family	Ht.	Family	Ht.
418	2	14.5	2	8.5	5	14.1
	1	13.6	3	6.6	1	14.0
	3	9.7	1	6.0	4	12.7
	4	9.2	5	6.0	2	10.9
	5	8.6	4	5.6	3	10.7
236	4	16.7	3	8.8	1	12.2
	1	16.4	4	8.5	4	12.2
	2	16.1	1	7.9	5	11.8
	5	15.4	5	7.2	2	11.4
	3	13.9	2	6.8	3	9.6
315	3	15.3	3	10.2	4	16.1
	4	13.4	4	6.9	2	15.2
	5	12.8	5	6.6	5	14.4
	2	10.8	1	6.6	1	14.1
	1	9.2	2	6.6	3	13.3
348	3	14.4	4	7.1	5	14.6
	5	13.6	3	6.0	4	11.6
	4	13.5	1	5.9	1	11.2
	2	10.3	2	5.9	3	11.0
	1	10.1	5	5.3	2	9.8
427	5	17.2	5	9.3	3	13.0
	3	14.7	4	7.6	2	12.9
	4	14.0	1	7.2	5	11.9
	2	12.5	3	6.2	4	11.2
	1	11.5	2	5.4	1	10.6
436	5	15.7	3	8.7	3	21.1
	1	13.8	2	7.5	2	16.0
	4	13.4	5	7.4	1	15.6
	3	12.9	1	6.8	4	13.5
	2	12.2	4	6.7	5	10.2
431	2	13.9	1	7.6	4	14.8
	1	12.7	4	7.1	1	13.6
	5	12.1	2	6.9	3	13.1
	3	10.9	5	6.0	5	13.0
	4	10.7	3	5.3	2	12.2

1/ Differences among families within sources significant at the 0.05 level in the southern planting.

2/ Differences among families within sources significant at the 0.05 level in the northern planting.

3/ Differences among families within sources significant at the 0.05 level in the central planting.

variation pattern found in Mississippi sweetgum occurs in other Gulf Coast states as well because the correlation of height growth with latitude is well-known in many other species. The east-west variation found in the present experiment is not predictable elsewhere, however, and may or may not occur in other sweetgum populations.

There is sufficient genetic variation within the present study area to make selection for increased growth rate in the Mississippi sweetgum population feasible. The variation occurs within sources, among sources, and among larger geographic areas; improvement strategy needs to take this into account. First of all, the optimum geographic area, or zone in which selection is to be based should be chosen (figs. 2-4). Gains in height growth of 1.8 feet in 10 years can be obtained by selecting sources in the Mississippi area. For plantings of improved stock in the southern or central part of Mississippi, the decision is straightforward--selection should be made in the A zone of Figs. 2 and 3. For plantings farther north, the seed collection zone should be shifted to the northwest.

Once the optimum zone is chosen, the next step is to make selections within it. The present results show source to source variation within the optimum zone, but no obvious pattern to it. Source performance commonly varies from well above the mean of the optimum zone to well below it in sources only 10-15 miles apart. Because adjacent sources rarely respond in the same way, there is no reason to believe there are groups or subzones of desirable sources. Conservative judgment, then, would have to be that performance of the progeny of the five trees sampled in each source represents no larger population than just those five trees. Thus, selection of individual parent trees should probably be at random over the entire optimum seed collection zone rather than in smaller areas.

This and other studies indicate that the best way to find superior sweetgum families is to progeny test random selections rather than search intensively for superior phenotypes. Cooper (1975) found no difference in height growth in the progeny of sweetgum trees intensively selected for height and the progeny of nearby comparison trees. An efficient selection system for fast growth would involve collecting seed from many average or better phenotypes from throughout the optimum zone and establishing a progeny test within the planting zone. The number of parent trees selected should be limited only by the seed collection workload and the size of the progeny test that can be handled.

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GEOGRAPHIC PATTERNS OF ALLOZYMIC VARIATION IN LOBLOLLY PINE[1]

L. Zack Florence and George Rink[2]

Abstract.--Haploid maternal gametophytes from more than 200 loblolly pine (*Pinus taeda* L.) trees sampled from eight geographic provenances were assayed for six enzyme systems. Ten allozyme loci were identified having an average of 3.6 alleles per locus.

Results indicated considerable genetic differentiation has evolved within the loblolly pine species. Structuring of the species genetic variation may be a result of restriction to gene flow and varying selection regimes over the natural range of loblolly pine.

Additional keywords: Isozymes, environmental variation, gene frequency, regression, correlation.

INTRODUCTION

It is well documented that the electrophoretic analysis of isozymes is applicable to the study of genetic variability in forest tree populations (Rudin, 1976). The direct estimation of Mendelian gene frequencies in populations of the Pinacea is readily obtained from the simply inherited, codominant isozyme gene markers using the haploid (1N) maternal gametophyte. This study addresses two basic questions using this tissue and the isozyme technique: (1) how much genetic variability can be detected in the loblolly pine (*Pinus taeda* L.) genome when sampled across its natural range; and (2) how is the detectable genic variation distributed?

MATERIALS AND METHODS

Sample Locations.--Gametophyte tissues from more than 200 loblolly pine trees were assayed in the study. These included 195 single-tree collections and two bulk-seed lots representing at least 5-10 trees each.

The range map (Figure 1) shows the locations of the 75 local populations from which ≥1 tree was analyzed. Eight geographic provenances of loblolly pine were available: Central Texas (TXC), East Texas (TXE), Arkansas (AR), Louisiana (LA), Mississippi (MS), Alabama (AL), Georgia (GA), and South Carolina (SC).

Mean longitude, latitude, and means of six environmental variables were calculated for each of the eight loblolly pine provenances (Table 1). These data were tabulated to describe the average environmental regime for a provenance.

Seed materials from contributors outside Texas were most helpful and are listed in the "Acknowledgments" of this paper. Seed collections were made from the two Texas provenances in the Fall of 1977.

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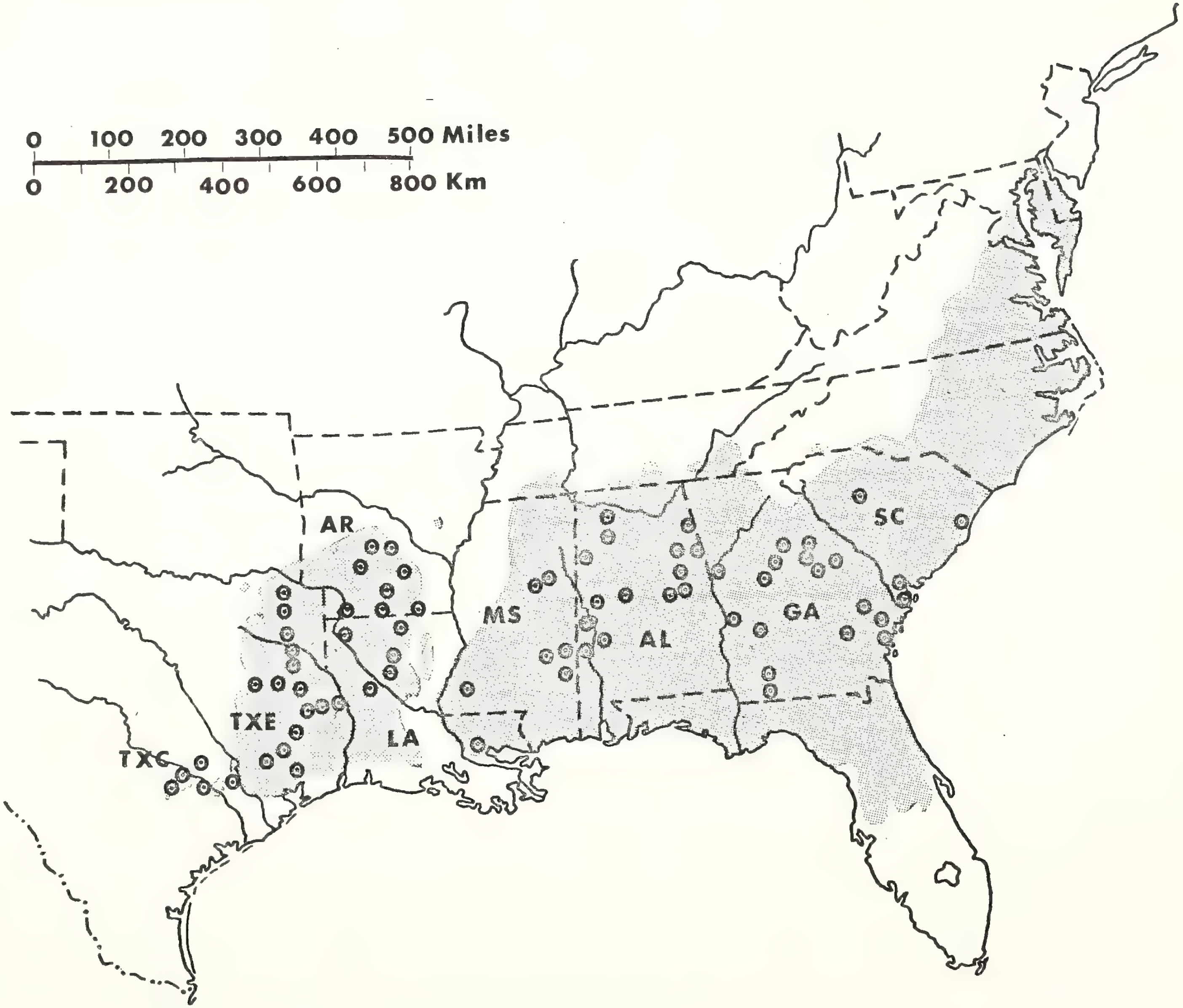


Figure 1. Seed sample locations of loblolly pine (range map from Critchfield and Little, 1966).

Table 1. Mean longitude, latitude and means for the environmental variables associated with each of the loblolly pine provenances.[1/]

Location	Long.	Lat.	Ann. Precip.[a]	T_{Max}[b]	T_{Min}[c]	$\frac{T_{Max} + T_{Min}}{2}$	$\frac{T_{Max}}{T_{Min}}$	Range $(T_{Max} - T_{Min})$
TXC	97°12'	30°02'	29.7	86.3	42.6	64.4	2.03	43.7
TXE	94°54'	31°38'	41.6	83.9	37.6	60.8	2.23	46.3
LA	92°10'	31°40'	66.5	81.2	48.4	64.8	1.68	32.8
AR	92°30'	33°44'	58.1	80.7	45.5	63.1	1.77	35.2
MS	89°40'	32°26'	70.1	79.4	46.5	63.0	1.71	32.9
AL	86°55'	33°11'	71.6	78.1	44.6	61.3	1.75	33.5
GA	83°09'	32°21'	58.1	80.1	49.6	64.9	1.61	30.4
SC	80°21'	33°20'	56.5	80.2	49.0	64.6	1.64	31.2

a = annual precipitation (inches)

b = maximum monthly temperature (F°)

c = minimum monthly temperature (F°)

TXC = Central Texas

TXE = East Texas

LA = Louisiana

AR = Arkansas

MS = Mississippi

AL = Alabama

GA = Georgia

SC = South Carolina

[1/] Data Source: U.S. Dept. of Commerce, Climatological Data Summaries for the States, 1975.

Enzyme Analyses.--Seeds were stratified ($4^{o}C$) for 30 days on moist filter paper. They were germinated at room temperature and the gametophytes prepared for electrophoresis after radicle emergence (approx. 3-5 mm).

Standard horizontal starch gel (12% w/v, Sigma Chemical Co., St. Louis, MO) procedures were followed (e.g., Conkle, 1972; Guries and Ledig, 1978) using two discontinuous buffer systems. Acid phosphatase (AcP), glucosphosphate isomerase (GPI), malate dehydrogenase (MDH), and 6-phosphogluconate dehydrogenase (6-PGD) were assayed after procedures reported by Namkoong, et al. (1979). Glutamate oxaloacetate transaminase (GOT) and glutamate dehydrogenase (GDH) were analyzed from the "Poulik" system of Schaal and Anderson (1974).

Enzymatic activity was identified with methods from the following sources: AcP (Shaw and Prasad, 1970); GPI, MDH, and 6-PGD (Guries and Ledig, 1978); GOT, GDH, (Schaal and Anderson, 1974).

Inheritance at allozymic loci was confirmed by testing for 1:1 segregations of allelic variants contained in the gametophytes of heterozygous trees. Comparisons were also available from other enzyme studies of loblolly pine (Adams and Coutinho, 1977; Conkle and Adams, 1977; Hunter [unpublished]).

Genetic loci were assigned capital letters, A, B, C,... with A being the most rapidly migrating. Alleles were numbered, 1, 2, 3...n, the number 1 allele being the fastest migrating for a given locus. Relative migration distances between alleles were referenced against the consistent band patterns of the hybrid yellow corn, "Truckers' Favorite" (Service Seed Co., Crystal Springs, Miss.), and the most frequent allele at a locus.

Data Analyses.--Allelic variation at loci having ≥ 3 alleles was combined such that each locus could be analyzed as having two alleles. This permitted a more straightforward treatment of the binomial properties of independently segregating alleles within a population, i.e., p = most frequent allele plus rare alleles, $q = 1 - p$ = frequency of the second most frequent allele, such that $p + q = 1$ (Li, 1955).

Allele frequencies (transformed to $\arcsin\sqrt{\text{percent}}$) were entered into simple regression analysis and Pearson's correlation coefficients calculated to test the null hypothesis that genic variability in loblolly pine was randomly distributed over the eight provenances. The independent variables were those shown in Table 1.

RESULTS

Ten (10) allozyme loci and 36 alleles (avg. 3.6 alleles/locus) were identified for the six enzymes assayed among the eight loblolly provenances. Loci and their allele frequencies are shown in Table 2.

Closer inspection of the data in Table 2 prompts these observations:

(a) Total alleles recorded for a particular locus were not present in all provenances. For those alleles at low frequency (i.e., < .100), absence is likely a function of sampling error.

(b) Considerable heterogeneity exists among provenances for a given allele at a locus, e.g., MDH - B_1 = .731 in Central

TABLE 2. Allele Frequencies Calculated for the Ten Allozyme Loci in Loblolly Pine from Eight Geographic Provenances.

Locus	Allele	TXC	TXE	LA	AR	MS	AL	GA	SC	Overall Freq.
AcP	1	0	0	0	0	.038	0	.017	.111	.015
	2	.308	.354	.150	.067	.238	.250	.133	.278	.248
	3	.654	.594	.650	.833	.676	.562	.667	.556	.646
	4	.038	.021	.050	0	.038	0	0	.056	.024
	5	0	.031	.150	.100	.010	.188	.183	0	.067
GDH	1	.987	.906	1.000	.967	.971	.979	.817	1.000	.943
	2	0	.021	0	0	.010	0	.033	0	.011
	3	.013	.073	0	.033	.019	.021	.117	0	.042
	4	0	0	0	0	0	0	.033	0	.004
GOT-A	1	0	0	0	0	.011	.062	.083	0	.020
	2	.218	.065	.400	.300	.130	.188	.300	.222	.246
	3	.782	.635	.600	.700	.859	.750	.617	.778	.734
GOT-B	1	.038	.167	.150	.100	.087	.062	.133	.056	.099
	2	.962	.812	.850	.900	.913	.938	.833	.889	.890
	3	0	.021	0	0	0	0	.033	.055	.011
GPI	1	1.000	.990	1.000	.967	1.000	.979	.983	.944	.989
	2	0	.010	0	.033	0	.021	.017	.056	.011
MDH-A	1	0	0	0	.033	0	0	0	0	.002
	2	.974	.969	.850	.934	.990	.938	.950	.944	.961
	3	.026	.031	.150	.033	.010	.042	.033	.056	.033
	4	0	0	0	0	0	.020	.017	0	.004
MDH-B	1	.731	.667	.750	.833	.457	.562	.533	.389	.604
	2	.244	.281	.150	.167	.476	.417	.467	.611	.358
	3	.013	.031	.100	0	.067	021	0	0	.031
	4	.012	.021	0	0	0	0	0	0	.007
MDH-C	1	0	0	0	0	0	.021	.017	0	.004
	2	1.000	1.000	1.000	1.000	1.000	.979	.983	1.000	.996
6-PGD-A	1	0	.011	0	0	0	0	.050	.111	.013
	2	.397	.375	.400	.400	.419	.500	.233	.278	.367
	3	.029	.023	0	.067	.181	.042	.233	0	.090
	4	0	.023	0	0	.029	.062	.017	0	.018
	5	0	0	0	0	0	0	0	.111	.004
	6	.574	.568	.600	.533	.371	.396	.467	.500	.508
6-PGD-B	1	.897	.875	.900	.900	.959	.979	.717	.944	.897
	2	.013	.031	0	0	.027	0	.267	0	.048
	3	.090	.094	.100	.100	014	.021	.016	.056	.055
N[a]		39	48	15	10	≥30[b]	24	30	9	ΣN≥205

a = Number of trees sampled /provenance

b = Contained bulked-tree samples

Texas and .389 in South Carolina. The variance test for homogeneity of a binomial distribution showed there to be significant heterogeneity among provenances at $P \le .05$ (Snedecor and Cochran, 1973; p. 240) at all loci except GPI and MDH-C.

(c) Trends in gene frequencies and the presence or absence of alleles at a locus are somewhat partitioned west of the Mississippi River (TXC, TXE, AR, LA) and to the east (MS, AL, GA, SC). This observation was confirmed by correlation and regression analysis (note Tables 3 and 4).

(d) East Texas (TXE) and Georgia (GA) provenances contained the highest proportions of the total alleles recorded per locus over all provenances, 80.5 and 88.8 percent, respectively.

Pearson correlation coefficients and simple regression analyses were used as statistical procedures to determine the strength of association between provenance variables in Table 1 (x = independent variable) and gene frequency (y = dependent variable). These results are summarized in Tables 3 and 4.

When gene frequencies for all loci were tested over all provenances, only MDH-B had a marginally significant relationship with longitude. Visual inspection of gene frequency plotted against each provenance variable prompted all subsequent analyses to be performed with the data treated as either Western (TXE,TXC, AR, LA) or Eastern (MS, AL, GA, SC). Regression following this method of classification improved considerably the fit of the MDH-B data and was generally more informative for more loci. It also seemed consistent with the natural partition of the loblolly pine range (note Figure 1).

Table 3.--Significant Pearson Correlation Coefficients between most frequent allele per allozyme locus and provenance variables.

Provenances	Locus	Provenance Variable	Correlation Coefficient (r) [a]
Western	GDH	$T_{max} + T_{min}/2$	+.932
	MDH-A	Latitude	-.922
	MDH-B	T_{min}	+.961
	MDH-B	T_{max}/T_{min}	-.994
	MDH-B	$T_{max}-T_{min}$	-.998
	6-PGD-A	$T_{max}+T_{min}/2$	-.904
	6-PGD-B	Longitude	+.972
	6-PGD-B	Ann. Precip.	-.958
	6-PGD-B	T_{max}	+.973
Eastern	GPI	Longitude	+.901
	6-PGD-A	T_{min}	+.924
	6-PGD-A	T_{max}/T_{min}	-.948
	6-PGD-A	$T_{max}-T_{min}$	-.967

[a] Significance level: $P \le .05$

Table 4.--Summary of significant regressions of the most frequent allele per allozyme locus against provenance variables.

Provenances	Prov. Var. (x)	Locus (y)	r^2 [a]	$\hat{y}$
Western	T_{min}	MDH-B	.92	23.04 + .92(x)
	T_{max}/T_{min}	MDH-B	.99	174.92 -1.35(x)
	$T_{max}-T_{min}$	MDH-B	.99	89.42 - .67(x)
	Longitude	6-PGD-B	.98	54.03 + .19(x)
	Ann. Precip.	6-PGD-B	.96	73.28 - .03(x)
	T_{max}	6-PGD-B	.98	57.72 + .17(x)
Eastern	Ann. Precip.	6-PGD-A	.95	147.65 -1.54(x)
	$T_{max}-T_{min}$	6-PGD-A	.93	315.12 -8.32(x)

[a] Significance level: $P \leq .05$

DISCUSSION

The results presented above confirm the observations made by others in concluding that loblolly pine possesses considerable genetic variability at allozymic loci (Conkle and Adams, 1977; Hunter [unpub.]). Most striking is the degree to which the genic variation in loblolly pine has become organized in different regions of its distribution. It seems appropriate to believe that the genetic evolution of the species has been significantly influenced by the Mississippi River disjunction and subsequent development of environmental differences east and west.

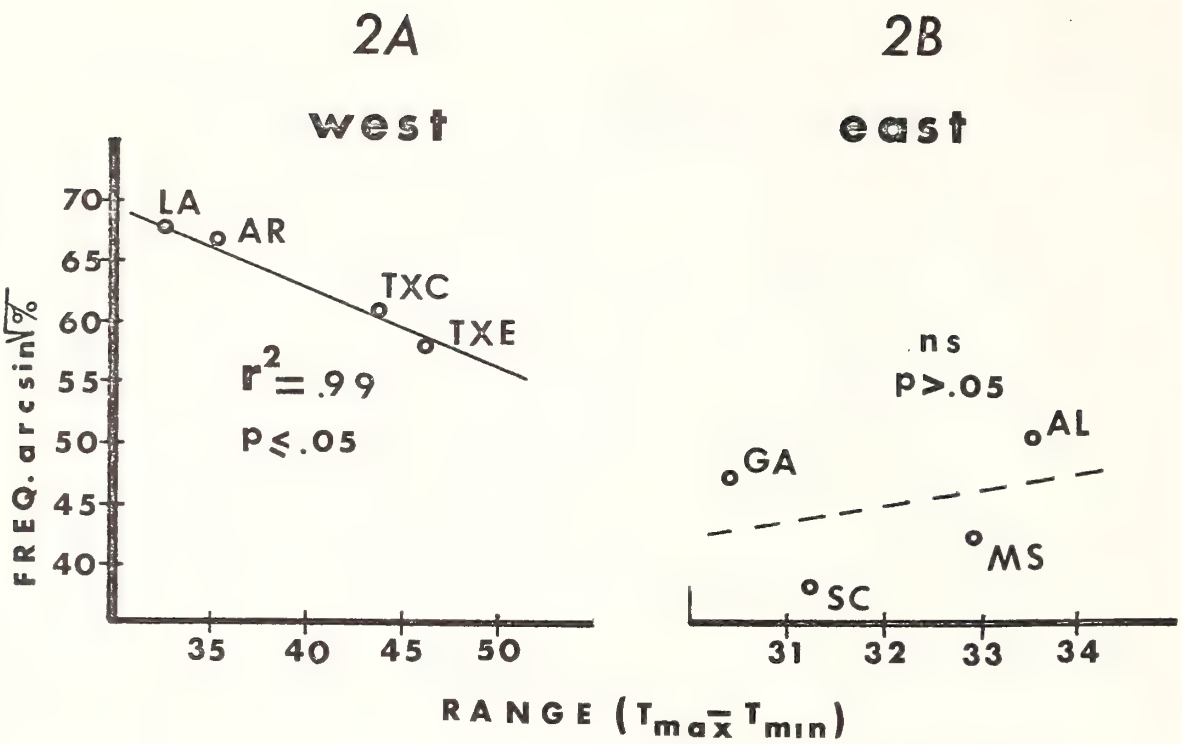
Some of the most obvious generalizations from the results of this study are:

(a) The overall environmental regimes in the western provenances of loblolly pine are more extreme in temperature and moisture. The eastern environment is somewhat more equable and tends to reflect more of a coastal influence.

(b) Three of the 10 allozyme loci, MDH-B, 6-PGD-A, and 6-PGD-B offer potential as gene markers of gene flow restriction and differential selection among the varying environments across the range of loblolly pine.

The observations made in (b) above are strikingly displayed in Figures 2A and 2B, showing the most frequent allele frequency for the MDH-B locus regressed against temperature range ($T_{max}-T_{min}$). These two representations graphically show the differential response of the same locus interacting with different sets of environmental patterns and likely, the MDH-B alleles having considerably different genetic backgrounds among the provenances.

Sampling strategy of this study maximized area of the natural loblolly range, rather than local genic variation and population structure. Therefore, many of the differences among populations within provenance have not been detected. However, it is significant to note that the relationships encountered



Figures 2A and 2B.--Regressions of the most frequent MDH-B allele against temperature range for loblolly pine provenances east and west of the Mississippi River.

in the present study coincide closely with the conclusions drawn from provenance studies of drought resistance (Knauf and Bilan, 1974), variation in height growth, volume, seedling survival and resistance to fusiform rust (Grigsby, 1977; Rink and Thor, 1971; Wells and Wakeley, 1966). If our results prove to be indicative of the allyzymic variation among local populations of loblolly pine, allozymic markers offer considerable potential during basic adaptational studies and monitoring selection efforts of tree improvement programs.

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VARIATION AND ESTIMATED GAINS IN HEIGHT, DIAMETER, AND VOLUME GROWTH FOR OPEN-POLLINATED PROGENY OF VIRGINIA PINE (Pinus virginiana Mill.)

David Todd and Eyvind Thor [1/]

Abstract.--Ten-year old open-pollinated progeny of random trees from 12 stands in Tennessee and Kentucky were analyzed for height, diameter, and volume growth. Approximately 20,000 individual progeny representing 128 half-sib families outplanted at three locations in Tennessee were measured. Variance componenets indicated that most of the variation in height, diameter, and volume growth was among half-sib progeny within families. However, the among family and among stand variance components made significant contributions to the total variation. Interaction variance components for locations with parent stands, and locations with families within stands were low for all variables; these components did not exceed 1.5% of the total variation. Two plantations were marked from conversion to seedling seed orchards. Gains in volume growth by selecting the best one third of the families and the best individuals within these families were estimated to be 18% and 30%.

METHODS

Twelve natural stands were selected from the Coastal Plain, Cumberland Plateau and Mountains, and the Great Valley physiographic regions of Tennessee and Kentucky (Figure 1). Stands were even-aged and of average or better than average quality. These stands ranged in age from 28 to 53 years and site indices varied from 60 to 87 feet (Thor, 1964). Only one stand (stand 10) had received any silvicultural treatment; this stand was a United States Forest Service seed production area which had been thinned heavily to remove undesirable trees.

From each stand 15 trees were selected as potential parent trees. Parent trees were healthy dominants or codominants with poor, average, or excellent phenotypic characteristics.

Originally, six open-pollinated progeny plantations were established. However, for this study only three plantations were used (Ames Plantation, Camp York, and Highland Rim) (Figure 1). Only 128 parent trees yielded enough seedlings to be included in the experiment and the number of progeny varied so much that only the Highland Rim plantation included all 128 families. Ninety families were represented at the other two locations.

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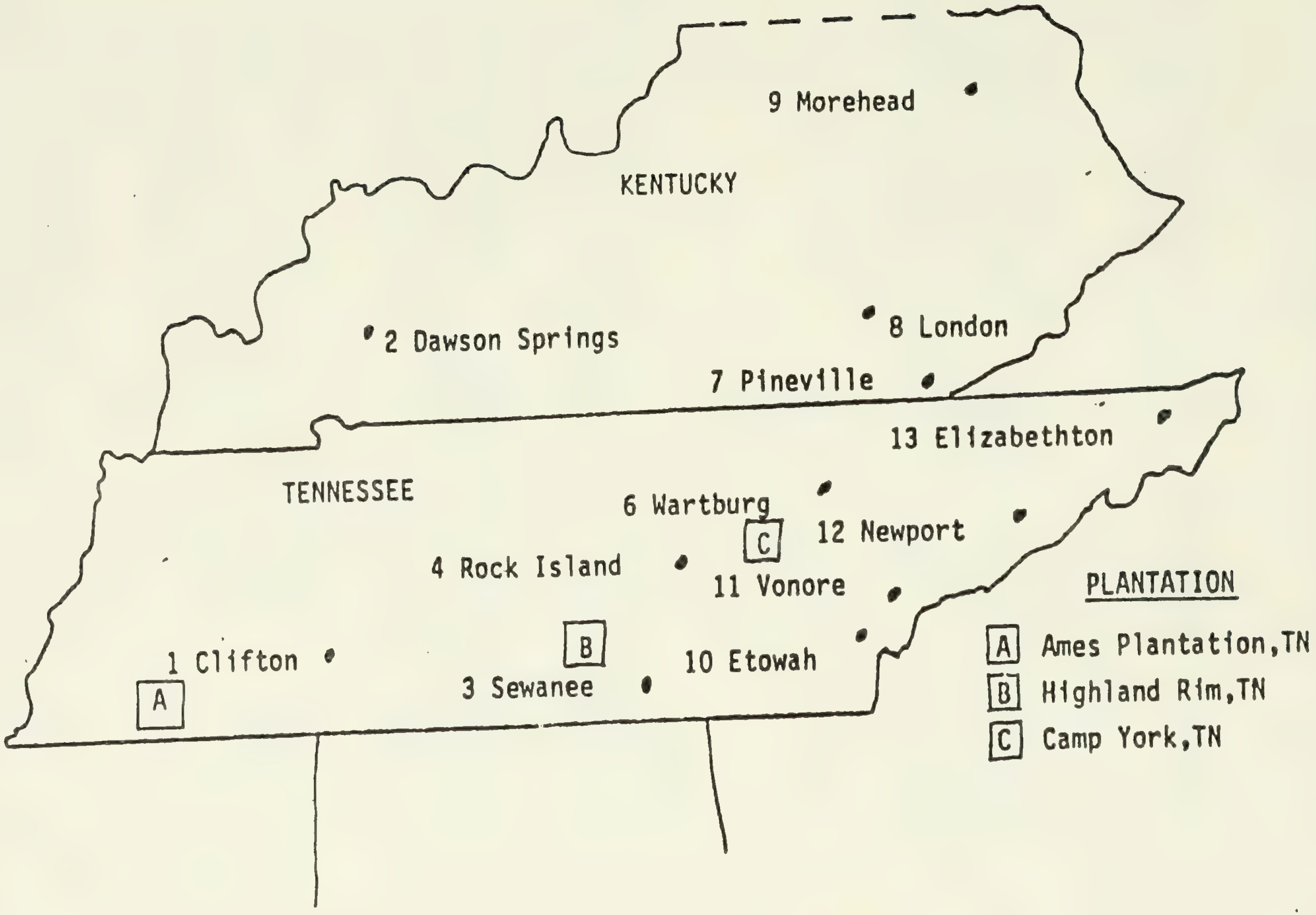

Figure 1. Location of parent stands and plantation sites.

Plantations consisted of seedlings planted in ten-tree family row plots arranged in a randomized complete block design. Each block was replicated ten times at each plantation. Spacing was four feet within family-row plots and eight feet between rows.

Measurements were made between late summer 1977 and spring 1978. Ten-year measurements included total height to the nearest foot and stem diameter (D.B.H.) to the nearest 0.1 inch. Individual tree volumes were computed from height and diameter measurements using a volume prediciton equation for young Virginia pine (Goebel and Mathews, 1966).

Analysis of variance was performed on an individual tree basis for each characteristic at each location and across all locations. All effects were assumed to be random. The analysis of variance was computed using the General Linear Model (GLM) procedures of the Statistical Analysis System (SAS 76) program (Barr et. al, 1976). The individual location and the combined location analyses, with some exceptions, followed those used by Rink and Thor (1976).

RESULTS AND DISCUSSION

Individual Locations

Mean squares, degrees of freedom, and levels of significance for volume, height, and diameter are presented in Table 1. At all locations the effects of stands and families-within-stands were significant for all variables.

Estimates of variance components, heritabilities, and standard errors are presented in Table 2. The variance components and heritability estimates for the Ames and Highland Rim plantations were similar. At Camp York, however, larger estimates for the interaction of replication by family-within-stand and smaller estimates for the family-within-stand variance components for all variables were obtained. This resulted in lower heritability estimates at Camp York.

Standard errors for the family-within-stand variance components and for the heritability estimates were in most cases small. The average standard error for both estimates was about 20% of the estimate. Since all families are not represented at all locations, differences in variances among test sites are partially attributed to variance of uncommon families.

Combined Locations

Mean squares, degrees of freedom, and levels of significance for volume, height, and diameter are presented in Table 3. Sensitivity of the experimental design is evident by the predominance of significance for almost all sources of variation and variables.

Table 1. Sources of variation, degrees of freedom, mean square, and levels of significance for Ames, Camp York, and Highland Rim locations.

Source	d.f.	Volume	Height	Diameter
Ames				
Replication	9	.5507**	197.1803**	1.3880NS
Stands	10	2.6814**	204.9419**	17.0351**
Replication x Stands	90	.0802NS	9.2225NS	.7008NS
Family within Stands	79	.3797**	42.7205**	2.7327**
Replication x Family within Stands	689	.0807**	9.6240**	.6722**
Within Plot	5551	.0697	5.3691	.6429
Camp York				
Replication	9	1.6418NS	348.6930**	3.9068**
Stands	9	3.8621**	88.0778**	17.0990**
Replication x Stands	81	.2268NS	16.0305NS	.9713NS
Family within Stands	80	.7085**	32.2690*	2.7416**
Replication x Family within Stands	685	.2356NS	24.9829**	1.0711**
Within Plot	4008	.2132	6.0741	1.0327
Highland Rim				
Replication	9	1.4775**	273.5270**	3.4109**
Stands	11	6.9285**	191.8290**	26.5132**
Replication x Stands	99	.2503**	11.7065**	.9095NS
Family within Stands	124	.9062**	36.7236**	3.4662**
Replication x Family within Stands	993	.1648NS	8.0030**	.6801NS
Within Plot	8995	.1848	4.9925	.8019

* Significant at the .05 level.
** Significant at the .01 level.
NS Nonsignificant at the .05 level.

Table 2. Variance components, heritability estimates, and standard errors for volume, height, and diameter growth for three locations. Numbers in parentheses indicate percentage contribution to the total variation.

	s^2_W	$s^2_{RxF/S}$	$s^2_{F/S}$	$S.E._{F/S}$ a/	s^2_{RxS}	s^2_S	s^2_R	h^2 b/	$S.E.(h^2)$ c/
Volume									
Ames Plantation	.0697 (87.3)	.0014 (1.7)	.0041 (5.1)	.0008	NC d/	.0039 (4.9)	.0007 (0.9)	.2189	.0425
Camp York	.2132 (90.5)	.0041 (1.7)	.0087 (3.7)	.0020	NC	.0066 (2.8)	.0029 (1.2)	.1539	.0354
Highland Rim	.1848 (90.2)	NC	.0098 (4.8)	.0015	.0010 (0.5)	.0071 (3.5)	.0021 (1.0)	.2014	.0308
Mean	.1559	.0018	.0075		.0010	.0072	.0019		
Height									
Ames Plantation	5.3691 (77.0)	.5868 (8.4)	.4561 (6.5)	.0927	NC	.2740 (3.9)	.2879 (4.1)	.2845	.0578
Camp York	6.0741 (57.8)	3.4887 (33.2)	.1345 (1.3)	.0962	NC	.1327 (1.3)	.6816 (6.5)	.0555	.0397
Highland Rim	4.9925 (79.9)	.3993 (6.4	.3809 (6.1)	.0615	.0433 (0.7)	.1772 (2.8)	.2554 (4.1)	.2639	.0426
Mean	5.4786	1.4916	.3238		.0433	.1882	.4083		
Diameter									
Ames Plantation	.6429 (91.7)	.0040 (0.6)	.0284 (4.1)	.0059	.0005 (0.1)	.0240 (3.4)	.0010 (0.1)	.1682	.0349
Camp York	1.0327 (93.4)	.0071 (0.6)	.0308 (2.8)	.0080	NC	.0296 (2.7)	.0060 (0.5)	.1151	.0299
Highland Rim	.8019 (92.1)	NC	.0369 (4.2)	.0058	.0027 (0.3)	.0267 (3.1)	.0024 (0.3)	.1760	.0276
Mean	.8258	.0040	.0320		.0011	.0268	.0031		

a/Standard error of the family-within-stand variance component.

b/Heritability = $\frac{4s^2_{F/S}}{s^2_W+s^2_{RxF/S}+s^2_{F/S}}$

c/Standard error of the heritability estimate.

d/NC=negative estimate of component.

Table 3. Sources of variation, degrees of freedom, mean squares, and levels of significance for volume, height, and diameter growth for combined locations.

Source	d.f.	Volume	Height	Diameter
Locations	2	281.1293**	75,820.0927**	432.2160**
Replication within Location	27	1.2234**	273.1334**	2.9019**
Stands	11	9.8113**	352.2290**	45.6821**
Location x Stands	19	.8145**	39.2409NS	3.3085**
Stand x Replication within Location	270	.1865**	12.1757**	.8585
Families within Stands	125	1.3372**	67.6670**	5.6565
Location x Families within Stands	159	.2536**	13.7791**	1.1271**
Replication within Location x Families within Stands	2367	.1608**	10.2223**	.7909NS
Within Plot	18554	.1565	5.3388	.8044

** Significant at the .01 level.
NS Nonsignificant at the .05 level.

Estimates of variance components, heritabilities, and standard errors are presented in Table 4. Although not directly comparable, the estimates obtained from the combined analysis and the mean of the estimates obtained from the individual locations are of the same magnitude.

The analysis indicates that for all variables the within-plot variance components accounted for the largest portion of the phenotypic variance, representing 91.7% for volume, 77.8% for height, and 93.1% for diameter. Location components of interaction (location by stand, and location by family within stand) are very small; together these accounted for only 1.0% for volume, 1.5% for height, and 1.1% for diameter of the phenotypic variation. Heritability estimates were .17 for volume, .20 for height, and .4 for diameter.

When tenth-year results are compared to the fifth-year results obtained by

Table 4. Variance components, heritability estimates, and standard errors of the family-within-stand variance components and heritability estimates for volume, height, and diameter for combined locations. Numbers in parentheses represent the percentage contribution to the phenotypic variation.

Variance Components	Variables Volume	 Height	 Diameter
s_S^2	.0050(2.93)	.1494(2.18)	.0210(2.43)
s_{LxS}^2	NC [a/]	.0391(0.57)	.0035(0.41)
$s_{F/S}^2$	.0067(3.92)	.3417(4.98)	.0287(3.32)
S.E.$(s_{F/S}^2)\pm$ [b/]	.0011	.0538	.0045
$s_{LxF/S}^2$	.0017(1.00)	.0676(0.98)	.0064(0.74)
$s_{R/LxF/S}^2$	.0008(0.47)	.9279(13.52)	NC
s_W^2	.1565(91.68)	5.3388(77.77)	.8044(93.10)
h^2 [c/]	.1664	.2048	.1379
S.E.$(h^2)\pm$ [d/]	.0265	.0322	.0214

[a/] NC = negative estimate of component.

[b/] Standard error of the family-within-stand variance component.

[c/] $$h^2 = \frac{4(s_{F/S}^2)}{s_W^2 + s_{R/LxF/S}^2 + s_{LxF/S}^2 + s_{F/S}^2}$$

[d/] Standard error of the heritability estimate.

Rink and Thor (1976) there is considerable similarity. The only consistent difference is the slightly lower proportion of the phenotypic variation accounted for by the stand variance component at ten years than at five years.

Ranking the stands by volume growth revealed that three stands (stand 10, Etowah, Tennessee; stand 1, Clifton, Tennessee; and stand 11, Vonore, Tennessee) consistently ranked first, second and third at all locations. Although stand 12, Newport, Tennessee, ranked second at the Highland Rim location, it was only represented in this location.

APPLICATION OF RESULTS

Two of the progeny plantations, Ames and Camp York, were marked for conversion to seedling seed orchards. This was accomplished by selecting the best families and the best individual within a selected family row plot. Selected families were based on their performance across all locations. Although volume growth was the main selection criterion, individuals with poor stem form were not accepted, thereby possible sacrificing some volume gain.

Individual tree heritabilities (h_I^2) are appropriate in the estimation of genetic gains only when individuals are selected based on individual performance, as in mass selection. When entire families are selected and rejected based on the mean of the family individuals and when individuals are selected or rejected based on their deviation from the family mean, then individual tree heritability estimates cannot be applied to these separate stages of selection to estimate gains. Falconer (1960) presented a method for computing gains resulting from family and within-family selection. This method computes heritability for family means (h_F^2) and heritability for individuals within family (h_W^2) in terms of individual heritability (h_I^2).

$$h_F^2 = h_I^2 \cdot \left[\frac{1+(n-1)r}{1+(n-1)t}\right]$$

$$h_W^2 = h_I^2 \cdot \left[\frac{1-r}{1-t}\right]$$

where: n = family size
r = .25 for half-sibs
t = intraclass correlation of family members.

Expected gains from both plantations are presented in Table 5. The selection differential (SD_F) between the mean of selected families and the location mean was multiplied by the family mean heritability (h_F^2) to obtain an estimate of gain (G_F) from family selection.

$$G_F = SD_F h_F^2$$

Table 5. Expected gains in volume growth (ft.^{3}) from selecting the best individual within a given family at Ames and Camp York. Numbers in parentheses indicate percentage contribution at each stage of selection.

Item	Ames	Camp York
1. Location Mean Volume (ft.^{3})	.5492	.9505
2. Mean Tree Volume (ft.^{3}) of the Selected Families	.6600	1.0900
3. Mean Tree Volume of the Selected Trees Within the Selected Families	1.0747	1.6907
4. Selection Differential for Selected Families	.1108	.1395
5. Selection Differential for Selected Trees Within Families	.4147	.6007
6. Number of Families Selected	27 of 90	28 of 90
7. Volume (ft.^{3}) Gain for Family Selection	.0921 (16.77%)	.0995 (10.47%)
8. Volume (ft.^{3}) Gain for Within Family Selection	.0721 (13.12%)	.0721 (7.58%)
9. Total Volume (ft.^{3}) Gain	.1642 (29.9%)	.1716 (18.05%)

Likewise, the selection differential (SD_W) between the mean of the individuals selected within selected families and the mean of the selected families was multiplied by the within family heritability (h_W^2) to obtain an estimate of gain (G_W) from within-family selection.

$$G_W = SD_W h_W^2$$

Since these gains are additive, the total gain is the sum of the gain obtained from each stage of selection. Expected volume growth gains from Ames and Camp York plantations by selecting 27 or 28 of 90 families at each location and the best individual within each of these families was .1642 $ft.^3$ and .1716 $ft.^3$, respectively. The volume gain was 29.9% at Ames and 18.0% at Camp York above the population mean at each location.

Estimates of volume growth gain based on a hypothetical roguing of the Highland Rim location were also made using the method described by Falconer (1960). By selecting 30% of the families and the best individual within those families, the total volume growth gain was estimated to be 25.8% above the location mean. Similar results, 25.1% above the location mean, were obtained by using the variance component method of multistage selection described by Namkoong et al. (1966) as adapted by Evans and Thor (1971).

Based on ten-year data, the most promising seed sources appear to be those from the central part of the Great Valley of Tennessee. In addition, substantial improvement in volume, height, and diameter growth can be obtained through a selection breeding program in Tennessee for Virginia pine. Volume gains from seedling seed orchards compare favorably with those reported from grafted orchards of other southern pines.

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AVOID EARLY SELECTION FOR GROWTH RATE IN COTTONWOOD

D. T. Cooper and Robert B. Ferguson[1/]

Abstract. A sample of 37 cottonwood clones from a selection program was compared with a sample of 40 random clones in a 14-year test at two sites near Stoneville, Mississippi. Throughout the test period, the select sample was slightly better in mean growth rate, but this difference decreased with age. Performance of "blue tag" clones selected at age 5 and planted commercially was good. But a group of clones selected at age 14 showed from two to three times as much improvement in diameter and height as the group selected at age 5.

Eastern Cottonwood (Populus deltoides Bartr.) is an important, fast growing plantation hardwood in the South. Because of its widespread occurrence, high variability, large number of seeds per catkin, and ease of vegetation propagation, many more genotypes can be assembled than can be evaluated adequately. In most breeding programs many genotypes are eliminated after only minimal evaluation, and such rapid elimination can result in the loss of much useful variability. In the long run, expedient selection may prove more costly, as results from a 14-year clonal test near Stoneville, Mississippi, illustrate.

MATERIALS AND METHODS

We studied two populations of clones. Twenty-five female parent trees with good growth and form were selected in various stands along the Mississippi River from 50 miles north to 50 miles south of Greenville, Mississippi. This was followed by selection in the nursery from among 160 seedlings from open-pollinated seed from each of these trees. One or two stages of one-year clonal tests were used to select the 37 most promising clones from these 4,000 seedlings. The other population was sampled by cloning 40 random trees from a total of six natural stands from 2 to 4 years old along the same segment of the river. The two samples represented the practical extremes of selection intensity that might be represented in preliminary cottonwood clonal test outplantings.

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In 1965, the clones were outplanted in 4-tree linear plots with 10 x 10 ft. spacing. A randomized-complete-block design with 5 replications was used at each of two locations. One outplanting was made on Sharkey clay soil at the Delta Experimental Forest (DEF) near Stoneville, Mississippi. The other was on Commerce silt loam soil at Huntington Point (HP) 10 miles north of Greenville, Mississippi, and about 20 miles from the first site. Both sites have comparable rainfall and temperature patterns. Differences in growth rates presumably would result mainly from differences in soil type. These two soil types bracket the range of soil types likely to be planted to cottonwood in the Lower Mississippi Valley. Both sites were planted with 20-inch unrooted cuttings of comparable quality, with 3 cuttings planted per spot. To improve uniformity, each spot was thinned to the best tree in June of the first growing season. Both sites were clean-cultivated the first year.

The HP location was thinned at age 3 by removing alternate rows across clones. The poorer of the two remaining trees per plot was removed at age 5. A third thinning occurred at age 8 when a few of the poorest remaining trees, those most likely to be crowded out, were removed, resulting in some missing plots. At DEF the single thinning consisted of removing alternate rows across clones at age 3.

Analyses of variance and covariance based on plot means were conducted separately for the select and the random samples within and between locations. Components of variance and covariance were computed from the mean squares and mean products for use in computing broad sense heritabilities, genotypic gains, and genotypic correlations. Clones not present in at least 3 of 5 replicates at both locations were omitted from analysis of variance, leaving 30 select clones and 27 random clones.

RESULTS AND DISCUSSION

Growth rate at DEF was poor, resulting at age 14 in less than half the height and diameter at HP (44 ft. vs 90 ft.; 5.7 in. vs 12 in.). Since sites now being recommended for cottonwood often are similar to the HP site, with possibly a slight tendency toward the soil characteristics of DEF, our main interest is in the results from HP.

Throughout the 14-year test, the selct sample was slightly better in mean growth rate than the random sample (Table 1), but this difference decreased with age. Variation among clones for diameter was similar for the two samples (Table 2). The random sample was somewhat more variable for height than was the select sample. Since means were not greatly different, superior clones probably could be selected from either population. However, those clones that were best for height and diameter at both locations were from the select sample.

Table 1.--Mean performance of the select sample as a percentage of the random sample mean for height and diameter at each location.

	HP		DEF	
Age	D.b.h.	Height	D.b.h.	Height
1	110	108	107	108
2	111	107	114	109
3	109	106	109	107
4	109	---	106	---
5	108	106	104	---
6	108	---	103	---
7	108	106	102	104
8	108	---	---	---
14[a]	101	102	98	101

[a] Values across the table would be 105, 106, 101, and 104 if all clones rather than only those remaining in 3 or more replications at both locations were included.

Table 2.--Estimates of Genotypic (σ^2_C) and Genotype - environment (σ^2_{CE}) components of variance.

	Select sample population			Random sample population		
Character	σ^2_C	σ^2_{CE}	$\sigma^2_{CE}/$ $\sigma^2_C + \sigma^2_{CE}$	σ^2_C	σ^2_{CE}	$\sigma^2_{CE}/$ $\sigma^2_C + \sigma^2_{CE}$
Height						
age 3	1.039	.851	.45	2.050	.838	.29
age 7	7.081	2.224	.24	7.029	3.841	.35
age 14	17.378	12.395	.42	145.960	49.027	.25
Diameter						
age 3	.084	.038	.31	.067	.031	.32
age 7	.398	.230	.37	.217	.207	.49
age 14	1.018	1.068	.51	1.910	.504	.21

To determine whether clonal selection from the nursery or from very early replicated field tests would be effective in identifying clones with long-term growing potential, we examined data from the random sample. We found that by age 14 the top 25 percent of the clones for height or diameter at age 1 at DEF or HP were little better than random clones for height or diameter (Table 3). The genotypic correlation between measurements at age 1 and at age 14 was negligible.

Table 3.--Effect on performance at age 14 of selecting the top 25 percent of random sample for height or diameter at HP or DEF expressed as a percentage of the random sample mean.

	Performance at age 14			
	D.b.h.		Height	
Type of selection	HP	DEF	HP	DEF
Selection at age 1 for d.b.h.				
HP	104	103	100	102
DEF	108	104	101	101
Selection at age 1 for height				
HP	102	103	100	104
DEF	99	107	101	104
Selection at age 7 for d.b.h.				
HP	102	106	99	102
DEF	94	111	94	107
Selection at age 7 for height				
HP	101	105	98	103
DEF	98	110	98	106
Selection at age 14 for d.b.h.				
HP	113	102	104	99
DEF	100	113	98	106
Selection at age 14 for height				
HP	108	97	107	98
DEF	95	109	96	108

Because each clone was represented by 4 widely spaced trees in each of 5 replications at age 1, the data presumably were better and the small amount of improvement possible from selection greater than would occur from selection in nonreplicated field tests or in most clonal nursery evaluations that are close-spaced and replicated. However, little was accomplished by one-year evaluation.

Assuming selection at age 7 rather than age 1, we examined the random sample further. Clones in the upper 25 percent at age 7 for either height or diameter at each location were no better than the sample mean by age 14 at HP (Table 3). However, at DEF these tended to be superior at age 14.

Since the effects of selection in natural stands and in the nursery were confounded, only indirect methods of assessing their contributions in the select sample could be used. The reduction in superiority of the select sample with time could be due either to the tendency for early growth superiority from nursery selection to be poorly correlated with mature tree performance or to the increasing importance of the differences between natural stand environment and testing-site environment as plantation trees grew larger. These factors would tend to be offset by an increasing correlation between older plantation trees and natural stand trees. The importance of genotype-environment interaction increased little if any with age (Table 2), so it can be omitted as an important cause of change. For early selection, all that we can conclude is that the combination of selection in natural stands plus nursery selection resulted in a slight improvement in growth rate of about the same magnitude as that possible from selecting the upper 25 percent of a random population in a replicated, multiple-tree plot clonal test at age 1.

At age 5, 14 clones were chosen for possible commercial planting (Mohn et al., 1970). Eleven came from the select sample and three from the random sample. Five of these received "blue tag" certification and have become the primary cottonwood clones planted in the South. Mohn et al. (1970) pointed out that these clones were only partly tested, that risks were associated with their wide-scale planting, and that accurate predictions of their merits would require testing for at least half a timber rotation over a wide geographic area and on a range of sites for cottonwood planting. The clones are now about half the timber-rotation age.

The group of 5 blue-tag clones have grown 20 percent more rapidly in volume than has the random group, but a group could be selected that would have done much better (Table 4). For volume at age 14, the 4 best clones from the select sample, ST 66, ST 69, ST 70, and ST 72, averaged 74 percent better at HP, 65 percent better at DEF, and 71 percent better over both locations than did the random sample. Genotypic gain predictions were similar to actual values for individual locations but indicated that the 71 percent over both locations might be unrealistically high. When selecting the four best clones over such widely varying sites we can only expect gains of 23 percent over the select sample and 28 percent over the random sample. Nevertheless, the four best clones from our select population ranked at the top of HP and were among the 7 best at DEF. This performance suggests that development of clones with broad application is feasible, although the magnitude of genotype-environment interaction remains as important (Table 2) as it was at age 3, when Randall and Mohn (1970) recommended selection for specific sites.

Table 4.--Performance of clones and clonal groups at age 14 expressed as a percentage of the mean of the random sample.

Comparison Group	HP			DEF			Combined		
	D.b.h.	Ht.	D^2H	D.b.h.	Ht.	D^2H	D.b.h.	Ht.	D^2H
Random population	100	100	100	100	100	100	100	100	100
Selection population	101	102	104	98	101	106	102	102	105
Five "blue tag" clones[a]	106	105	118	110	107	129	107	106	122
Fourteen Stonveille select[b]	111	106	131	110	106	127	111	106	130
Four "best" clones[c]	123	115	174	120	115	165	122	115	171
Stoneville 72	138	121	230	128	120	196	135	121	219
Stoneville 109	84	90	63	119	121	171	95	100	90

[a] Consists of ST 66, ST67, ST 74, ST 92, and ST 109.

[b] Consists of ST 63, ST 66, ST 67, ST 70, ST 71, ST 72, ST 74, ST 75, ST 81, ST 91, ST 92, ST 107, ST 109, and ST 124, selected at age 5.

[c] Consists of ST 66, ST 69, ST 70, and ST 72, selected at age 14.

The disadvantage of early selection is illustrated further by the performance of ST 72, a clone in the new group of 4 "best" clones, and ST 109, one of the blue-tag clones planted widely.

At age 1, ST 72 ranked 23rd out of 37 for diameter and 18th out of 37 for height at HP. It ranked 15th out of 37 for diameter and 7th out of 37 for height at DEF. But, by age 14, it ranked first for both characters at both locations. It was 3 or 4 years old before it ranked in the upper 25 percent. ST 72 probably would have been discarded in a short-term preliminary test, yet by age 14 it had more than twice the volume of the mean of the select sample (Table 4).

ST 109 changed from about average at age 1 to one of the best by age 4. It retained that superiority at DEF, but at HP it slipped from third for diameter and fourth for height out of 40 clones in the random sample at age 5 to 26th out of 27 clones for both characters at age 14 and had only 63 percent of the volume of the random sample mean and less than 30 percent that of ST 72. Other data show that ST 109 is highly susceptible to diseases caused by Melampsora medusae Thüm. and Septoria musiva Peck, perhaps explaining its poor performance at HP. Loss of photosynthetic ability as a result of these diseases normally occurs late in the season when the more moisture deficient Sharkey clay at DEF is incapable of sustaining further growth. Thus, growth would not be affected at DEF, but it would at HP. Free from these diseases, ST 109 might have maintained its excellent early growth rate.

A substantial number of valuable clones undoubtedly were lost by outplanting only 37 of 4,000 clones. We can only speculate on the number. Perhaps, if nursery and single-year close-spaced clonal tests were totally ineffective, 99 percent of the good clones were never outplanted, and only the best 4 of 37 rather than the best 400 of 4,000 were saved. But if the best 4 of 4,000 rather than 4 of 37 had been saved, genotypic gain could have been twice as large.

Although it may be best to wait until age 14 or longer to choose clones for commercial use, breeders need to be able to identify superior clones by the time they flower (age 6 in the South) for crossing and at an earlier age for retesting. Errors in choosing clones for these purposes are less serious than those incurred in choosing clones for commercial use. Clues available at an early age would expedite breeding programs. Traits that contribute to an efficient crown seem particularly important. These may include early foliation, late defoliation, resistance to foliar diseases and insects, large numbers and size of leaves, dark green leaf color, branch and leaf characteristics that allow maximum interception of light, and characteristics that hasten the death of leaves or branches that no longer contribute to the development of the tree. Characters that are measurable at an early age at little cost, are highly heritable, and are correlated with later performance should be used as substitutes for very early growth measurements or as supplements to later growth measurements.

Early testing techniques can be only partly substituted for long-term testing; so, when possible, studies should be installed and managed to provide data over long periods. Except for careful choice of sites, adequate plot size, fire protection and a willingness to wait, long-term testing requires little extra effort.

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THE USE OF BREEDING GROUPS IN ADVANCED GENERATION BREEDING

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Abstract.--In a continuing tree breeding program inbreeding will occur after a fairly limited number of generations regardless of the mating design that is used. The available evidence strongly suggests that in many forest trees inbreeding is associated with a high degree of inbreeding depression. By dividing the breeding population into breeding groups and only crossing individuals contained within a breeding group, it is possible to confine inbreeding within a breeding group. The different breeding groups are and will remain unrelated to each other.

Seed produced commercially can then be outcrossed, by assigning one individual of each of nine or more breeding groups to a given seed orchard block.

It appears advantageous to use a complementary mating design, when making crosses within a breeding group. One set of crosses will be made to estimate GCA by means of a polycross using unrelated pollen. This will circumvent the problem of having to compare individuals with different degrees of inbreeding. The other set of crosses provides the trees for the next generation of selection.

The system used by the WGFTIP Cooperative is described to show how these ideas can be implemented.

Additional keywords: inbreeding, mating design, polycross

In order to evaluate different advanced generation breeding systems it is necessary to make a number of assumptions, that may not be entirely realistic, but that are essential for making comparisons. Let us examine these first.

1) The same breeding system is maintained over an extended number of generations. In other words, the same number of individuals is selected each generation; the same mating scheme is employed, regenerating the same number of families each time; and the intensity of selection is the same each generation. Although in practice this will never happen, one has to make this assumption to make valid comparisons and to avoid designing a system that will eventually self destruct.

2) No new material is brought in after the first generation selections have been made. Again this assumption is not realistic, but was adopted to

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facilitate comparisons, to evaluate the systems on their own merit, and because in advanced generations it will become increasingly difficult to bring in new material without losing much of the previously obtained genetic improvement.

Under these assumptions inbreeding starts to build up after a few generations in a small population. Let us take a hypothetical orchard with 50 clones as an example. Using the WGFTIP partial diallel mating scheme to produce the progeny tests, 100 families will be generated (Figure 1). Assumption 1 says we need to make 50 new selections for the second generation orchard. There are many ways of doing this, e.g., selecting 50 trees in the single best family, 25 trees in the two best families, etc. Let us assume we select the five best trees from the ten best families. The rate of inbreeding depends on the way in which the families are selected and is, therefore, somewhat unpredictable. A computer simulation indicates we can expect the results given in Table 1.

MALE

FEMALE	1	2	3	4	5	6	7	8	9	.	.	.	.	n
1		X	X											
2			X	X										
3				X	X									
4					X	X								
5						X	X							
6							X	X						
7								X	X					
8									X	X				
9										X	X			
.											X	X		
.												X	X	
.													X	X
n-1	X													X
n	X	X												

Figure 1. WGFTIP partial diallel mating scheme.

Inbreeding takes place at an average rate of slightly over three percent per generation. Although inbreeding obviously will not be a problem in our lifetime, as long as it takes about 20 years to produce a new generation, it does not take very many generations to reach significant inbreeding levels. If accelerated breeding procedures are developed allowing the production of a generation in less than 10 years, the problem could become serious more quickly.

Regardless of the time-frame the problem will force itself on us eventually and it would be much better if the researcher could establish positive control of the rate of inbreeding.

Table 1.--Results of computer simulation of inbreeding within a breeding population of 50 clones, assuming selection of the 5 best individuals of the 10 best families in each generation.

Generation	Average inbreeding coefficient	Inbreeding in least inbred family	Inbreeding in most inbred family
1	0	0	0
2	.0375	0	.125
3	.0594	0	.125
4	.113	.078	.188
5	.137	.102	.234
6	.168	.103	.264
7	.161	.123	.264
8	.208	.168	.288
9	.284	.226	.318
10	.307	.233	.358
11	.377	.335	.405

THEORETICAL FRAMEWORK

Theoretically one can distinguish several separate groups of trees in a breeding program: the trees grown for commercial wood production, the seed orchard, the progeny tests and the trees used for breeding. Each of these can have a different inbreeding level. For reasons of economy some are often combined, but they do not need to be. This is the key concept in devising a system to prevent inbreeding in the trees grown for commerical wood production.

Subdividing the Breeding Population

The seed produced from a seed orchard should be outcrossed, but the parents themselves may be inbred. To achieve outcrossing in the seed orchard even though parents may be inbred one only has to make sure that the parents are unrelated to each other. This can be accomplished easily by subdividing the selected trees in groups and not allowing crosses among trees belonging to different groups. This way the groups will remain unrelated forever. To establish an orchard only one selection of a given breeding group is represented in each orchard block. It is still possible to utilize several selections from a single breeding group by putting them in different blocks in the same orchard.

All controlled crosses for the purpose of producing advanced generation selections need to be confined to the breeding groups. As a result the breeding groups themselves will become inbred. One has the option of inbreeding rapidly or rather slowly. At the moment we are choosing to limit inbreeding to low levels. Inbreeding could be a useful tool, however, and some experimental work is needed to determine how well higher levels of inbreeding would work.

Use of Overlapping Generations

Once inbreeding is allowed a considerable degree of flexibility is added in choosing mating designs. Although it appeals to one's sense of order to keep each generation separate, this is not at all necessary. It might, for instance, be advantageous to use an exceptionally good first generation parent in crosses with second generation selections. This would lead to more rapid inbreeding, but could also generate more rapid genetic gain.

The Problem of Testing for General Combining Ability with Different Degrees of Inbreeding

If, as seems desirable, family selection is practiced, it is almost unavoidable that some families have different degrees of inbreeding than others. This would make the present partial diallel and tester schemes inappropriate for testing general combining ability, since general combining ability and inbreeding depression would become confounded. The problem could be circumvented, however, by using a polymix for testing general combining ability. Various kinds of polymixes would be possible, as long as they meet two requirements: 1) the pollen parents should be unrelated to the trees being tested. 2) The pollen should be as similar as possible to that expected in the orchard in which the selections are to be placed.

A Complete System

A complete system would, therefore, need to have the following elements:

1) A seed orchard in which each block contains one representative of each of nine or more breeding groups. A minimum of nine groups are needed if one wishes to maintain the present system of having two members of the same clone separated by at least two intervening positions.

2) A breeding population separated in unrelated breeding groups. The number of individuals in a breeding group is dictated by practical limitations. The lowest theoretical limit is one tree per breeding group. If we accept the need for a minimum of nine breeding groups a practical upper limit would appear to be around 100 trees per breeding group.

3) A complementary mating design (van Buijtenen, et. al., 1976) consisting of two separate sets of crosses each fulfilling a specific purpose: a) a set of polymix crosses to determine general combining ability, b) a set of specific crosses within the breeding group to produce a number of families from which to make selections for the next generation.

THE CURRENT IMPLEMENTATION IN WGFTIP

Because many of the clones in the WGFTIP are widely distributed, many members were using them in a large variety of crosses. Second generation selections obtained from these crosses would have had a high amount of relatedness. This relatedness would increase in future generations and make it difficult, if not impossible, to produce outcrossed seed in our production orchards.

First Generation Breeding Groups

To avoid this problem, the first generation breeding population has been divided into breeding groups. A clone belongs to only one breeding group irrespective of the number of orchards that contain that clone. Each breeding group contains approximately 25 selections, and it is anticipated that each cooperator will maintain four or five breeding groups for each of their orchards. When the base population is obtained, there will be approximately 32 breeding groups for slash and 96 for loblolly pine in our operating area.

The WGFTIP partial diallel crossing scheme will be utilized within each breeding group to complete the first generation breeding program (Figure 1). There will not be any control-pollination efforts across breeding group lines. Approximately 50 control-pollinated families will be generated within each breeding group. These controlled crosses will be field planted in three separate tests by the cooperator that is responsible for the breeding group.

Second Generation Breeding Groups

Second generation selections will remain in the same breeding group as their parents. To maintain a constant breeding population size, four or five trees from the best six families of the original 25 families will reconstitute the second generation breeding group. Because of our first generation crossing scheme, this will result in different degrees of relatedness among the second generation selections within a breeding group. Pedigree records will be maintained for each second generation selection.

Second Generation Mating Schemes

To evaluate the second generation selections, a complementary mating design will be utilized. A polymix cross will be used to evaluate the general combining ability of the selections. A separate pollen mix will be created for each breeding region. This pollen mix will remain constant over time and will be used for all of the second generation selections from the respective breeding region. A circular mating scheme will be used to produce material for the advanced generation selections that will form the breeding population for the third generation. Operationally, the circular mating design will be applied to a single breeding group which will contain approximately 25 selections. The general combining ability information obtained from the polymix progeny tests will determine which of the circular crosses will be used for the third generation selection activities.

The rate of inbreeding that occurs within a breeding group can be partially controlled by the arrangement of the clones in the circular mating design. Currently, our plans are to initially limit inbreeding during the early generations.

Field Layout of Progeny Tests

A different progeny test layout will be used for the different crossing schemes in the second generation breeding program. The polymix progeny tests will utilize a field planting design which will favor family evaluation for inclusion into production orchards. These progeny tests will be planted at a minimum of six locations, and they will be coordinated on a cooperative basis. The polymix progeny tests will sample the seed zone[1/] that the breeding group originated from and all of the seed zones where the selections may be utilized in production orchards. Individual cooperators will be responsible for progeny testing the circular mating tests for their breeding groups. These field tests will be designed to maximize the gains from within family selection efforts. An example would be to plant each cross in 100 tree block plots on three different sites.

Breeding Groups and Seed Orchard Designs

Production seed orchards will be designed in the WGFTIP standard ten clone block (Figure 2). Only one selection from a breeding group will be used in a given block within an orchard. Because there will not be any relatedness between breeding groups, the resulting seed will be outcrossed. Different blocks within a seed orchard can contain different selections from the same breeding group. By assigning selections from the same breeding groups to the same relative positions in two different orchard blocks, at least two intervening positions will be maintained between relatives in the production orchard. Because of the number of breeding groups per orchard type, selection intensity in developing an operational orchard can be applied at both the breeding group level and within the breeding group.

A	B	C	D	E	F	G	H	I	K
H	I	K	A	B	C	D	E	F	G
E	F	G	H	I	K	A	B	C	D
B	C	D	E	F	G	H	I	K	A
I	K	A	B	C	D	E	F	G	H
F	G	H	I	K	A	B	C	D	E
C	D	E	F	G	H	I	K	A	B
K	A	B	C	D	E	F	G	H	I
G	H	I	K	A	B	C	D	E	F
D	E	F	G	H	I	K	A	B	C

Figure 2.--WGFTIP - seed orchard block design. Each letter is assigned a different clone. All ramets of the same clone are separated by two intervening positions. A number of different blocks can be contained in any orchard (Langner and Stern 1955).

[1/] The WGFTIP operating area is divided into eight seed zones as follows: 1) northeast Texas, 2) southeast Texas, 3) north Arkansas, 4) south Arkansas, 5) north Louisiana, 6) south Louisiana, 7) north Mississippi and 8) south Mississippi.

CONCLUSIONS

1) The division of a breeding population into breeding groups insures that an operational tree improvement program will be able to produce outcrossed seed in advanced generation seed orchards.

2) A special mating design is needed in conjunction with the breeding groups. We chose to use a polymix cross combined with circular matings. Many other schemes would be possible.

3) Only one selection of each of ten breeding groups will be included in a given seed orchard block. Different blocks may include different selections of the same group.

4) The main advantages of this procedure are:

   a) Inbreeding due to relatedness among clones can be avoided in the seed orchard.
   b) The tree breeder assumes positive control of inbreeding, making it a tool rather than a liability.

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LONG-TERM TREE BREEDING

Hyun Kang[1]

Abstract.--Analysis of variance techniques are not useful for developing long-term tree breeding strategies. Therefore, tree breeders must use the information obtained from animal and crop experiments, and population genetics theories to develop long-term tree breeding strategies.

Additional keywords: Population size, gene model.

Many tree breeders are vitally interested in developing advanced generation breeding techniques because their breeding populations are entering the second generation. The development of such techniques is complex and requires a classification of the associated problems. Presented in this paper are examples of the information obtained from crop and animal genetic experiments and population genetics theories that can be used to develop long-term tree breeding strategies.

ANALYSIS OF VARIANCE

During the past 30 years, we have learned a great deal about analysis of variance. It has become evident that the existence of genetic variance is fundamental to successful tree breeding. We have also learned how to design mating schemes and field experiments and how to predict genetic gains for both direct and indirect selection systems. These techniques are designed to develop a picture of the variance structure of the breeding population(s) at a given point in time. The information obtained has then been used to help make breeding decisions for the immediately following generation. However, any linear projection of future population improvement based on the analysis of the picture at a given point in time is subject to severe errors if applied for more than three or four generations because the evolutionary process of populations is so complex and dynamic.[2] Furthermore, the analysis of variance classifies variances but does not describe the causes of the variances; consequently, many breeding principles cannot be developed by the use of analysis of variance.

TREE BREEDING BY INTUITION

Assuming that the proposition about the shortcomings of the analysis of variance is valid, are there other approaches which are as suitable to develop long-term tree breeding strategies in a fashion similar to the way the analysis of variance was to short-term tree breeding plans? The answer depends on the definition of the term "suitable". If it represents the accuracy of the point estimates of target parameters of the future, then the answer is "no". In developing long-term tree breeding strategies, the target parameters are not as important as they are in short-term tree breeding. For example, it is not realistic to ask what the average biomass production of loblolly pine at a typical North Carolina piedmont would be 4,000 years from now. It is more important to determine how to condition the breeding population so that it will express its maximum potential at the time of equilibrium while maintaining the capability to absorb shocks such as sudden changes in environments, intensity of forest management, breeding objectives, etc. Therefore, in long-term tree breeding, we are more interested in finding out the sufficient minimum conditions necessary for breeding rather than in setting definite targets for the future.

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[2] Many discussions of this kind can be found in articles published by Alan Robertson between 1960-1970. For example, Robertson (1961).

A good alternative to analysis of variance in long-term tree breeding appears to be the collective intuition of breeders and population geneticists. Although we might think that it is old, simple, and often irrelevant, collective intuition was the foundation on which we developed our estimation theory.

SOURCES OF INTUITION

To develop a long-term tree breeding strategy we must free our minds momentarily from the breeding populations and specific objectives we now have. Even if we know the genetic properties of our present breeding populations, they represent only a single static point of all the possible combinations of the factors within the boundary conditions. Such an understanding is not of much help in learning and using the population dynamics necessary for long-term breeding.

We can improve our intuition for advanced generation breeding in two ways: (1) by evaluating long-term breeding results obtained from crop and animal experiments, and (2) by learning and applying theoretical population genetics.

The breeding conditions of a crop (or animal) breeding experiment are likely to be different from that for trees. Likewise, the conditions are likely to be different among different crop (or animal) experiments. Therefore, results from a single experiment normally are not sufficient for making generalizations. It is possible, however, to find a more deterministic common denominator when several experimental results are assessed. A good example of this is from recurrent selection studies where many published results indicate that on the average the improvement of two phenotypic standard deviations of generation zero is easily obtained before the population average plateaus, regardless of the initial conditions and breeding techniques used. The example on selection for high oil content in corn from the textbook by Allard (1960) is a representative case of recurrent selection results (Figure 1). The figure vividly shows what is possible through recurrent selection. The area of overlap between the performances of individuals at generation zero and at generation ten is very small. Clearly, a tree breeder at generation ten cannot afford to go back to a natural population(s) for addition of genes to keep the genetic base broad because it will be difficult to find an individual that is as good as the average of the individuals in the tenth generation breeding population. Some other facts suggested by the graph are: (1) Continuous introduction of new individuals into

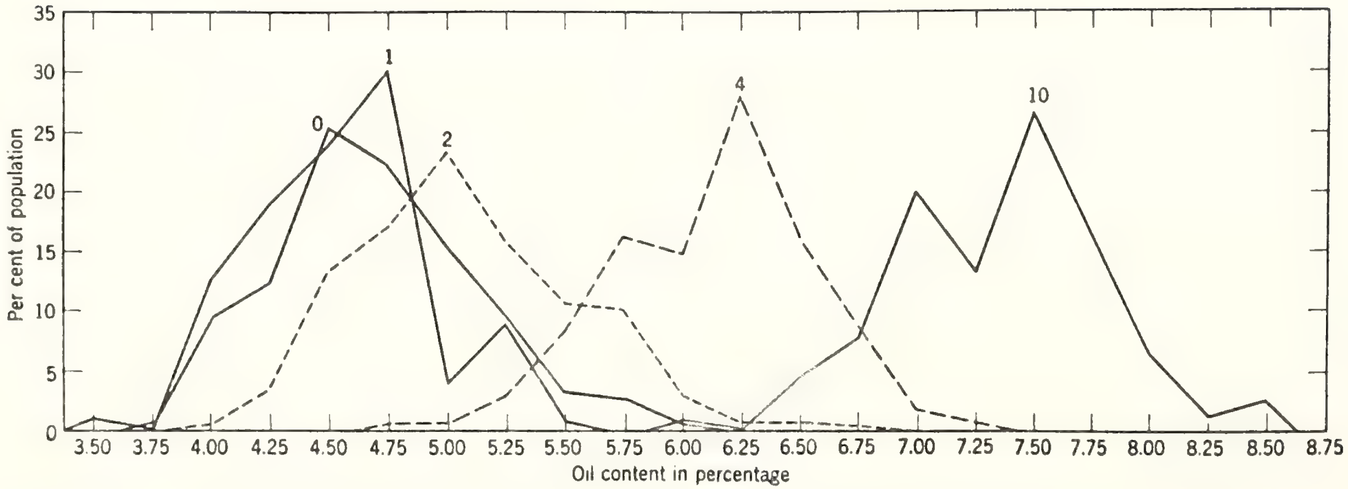

FIGURE 1. Selection for high oil content in corn. The frequency distribution of the original population is designated by 0 and the frequency distributions after various numbers of generations of selection by numbers. The mean oil content increased steadily with selection. Transgressive segregants appeared in the second-selected generation, and by the tenth-selected generation all individuals of the selected generations transgressed the original population. (After Smith, 1908.)

The above is an exact replica of Figure 16-1 of Allard (1960).
The reference for Smith (1908) from which it came is not found in the book.
(Reprinted by permission of John Wiley & Sons, Inc.).

the breeding population (open breeding population) is not a desirable option because it slows down the speed of the average population advance. (2) Repeated vegetative propagation preceded by selection is not an efficient long-term tree breeding method because the maximum gain after ten cycles of selection is limited by the distribution of the base population. (3) The maintenance of parallel breeding populations (whose ancestors may or may not overlap) under similar environments is a potential way of preparing for the future gene exchange need.

The recurrent selection research results, however, are not very useful for determining the necessary breeding population size. Most of the studies are not designed to answer this question and also it is not possible to obtain answers to some questions related to population size by experimental means.

Breeding population size can be determined through the use of population genetics theory. It is important, however, to understand that recommendations based on theoretical population genetics cannot be stated as positively as those of the previous example. The theories are developed from simple genetic models, while the structure of a real population is complex.[3/] As long as the limitation of the model is made clear from the beginning, population genetics theories are useful for improving intuitive breeding programs for forest trees.

Four simplified models will be used to illustrate the necessary population size for breeding. The breeding population size represents the number of selected parents used for mating.

(a) Major gene model

Under this model, the phenotypic expression of the trait of interest is determined by the genotype without environmental modification. If one locus influences the trait and the alleles act additively, the necessary population size will be one individual for monoecious species and two individuals for dioecious species. The population will reach its maximum potential in the trait of interest in one generation.

(b) Minor (quantitative) gene model

Under this model, a trait is influenced by genes at more than one loci and the expression of the genes is modified by the environment. If no linkage and no epistasis among genes at different loci is assumed (a simplifying but rather unrealistic assumption), it is possible to interpret the performance of the trait of interest in terms of the fixation probability of a favorable allele at a single locus. The probability is determined by initial gene frequency (q), degree of dominance (h), population size (N), and selection coefficient(s). Under gene action models other than over-dominance, the trait average is maximum when all the loci are fixed with the most desirable allele at each locus. The formula for computing the fixation probability

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[3/] A model does not have to be as complex as the real object it imitates; the main advantage of using models lies in their simplicity to show general trends.

(u(q)) is:

$$u(q) = \frac{\int_0^q \exp[-2Ns(2h-1)(1-x)x-2Nsx]dx}{\int_0^1 \exp[-2Ns(2n-1)(1-x)x-2Nsx]dx} \qquad \text{Kimura (1957)}$$

For simplicity, the formula can be evaluated as an additive model only (Table 1). The necessary population size decreases as the selection proportion decreases and the initial gene frequency increases. The necessary population size increases more rapidly between initial gene frequency .01 and .05 than for any other interval. Therefore, if we define the economic break-even point of initial gene frequency as .05 and ignore the rare alleles with smaller frequencies, we can conclude that the necessary population size for a minor gene is 85. A good review of this subject was made by Rawlings (1970).

Table 1. The necessary population size to fix the desirable allele in the population with 95% assurance*

Heritability .2
Number of loci 100

Initial gene freq. (%)	Proportion selected (%) under a truncation system				
	1	5	10	25	50
.01	281	364	426	590	937
.05	56	73	85	118	187
.1	28	36	43	59	94
.25	11	15	17	24	38
.5	6	7	8	12	18
.75	3	4	5	6	10
.9	-	2	2	3	4

*Additional steps, which were not detailed in the text, were used to develop the table using Kimura's formula.

(c) Independent neutral gene model

The neutral gene model is important to gene conservation. Many genes appear to be selectively neutral to a trait of interest, but they could play an important role if breeding conditions, product desires, or environment change. Because these genes are selectively neutral, the average probability of loss is not influenced by selection or by the population size. The probability of loss is 1-q. The population size, however, influences the speed of gene loss -- i.e., the smaller the population, the quicker the allele will be lost from the population (average). We can take advantage of the difference in rate to determine the necessary breeding population size. For example, a breeder might be willing to ignore the consequences of having a small population after a certain number of generations, say 100 generations or 4,000 years. Under this assumption the necessary population size can be obtained by modifying a formula given by Kimura and Ohta (1969) as follows:

$$N = -\frac{t(1-q)}{4q(\log_e q)}$$

This formula is subject to the condition that $N \geq \frac{1}{q}$ (Table 2). If we have neutral genes with $q = .05$, it will be necessary to have $N = 159$ to maintain this gene in the population for 100 generations.

Table 2. Population size necessary to maintain neutral genes with initial frequency q for t generations*

t (gen)	Initial frequency of neutral genes (q)								
	.005	.01	.02	.03	.04	.05	.1	.2	.5
10	-	-	-	-	-	-	10	6	4
20	-	107	63	46	37	32	20	12	7
30	282	161	94	69	56	48	29	19	11
40	376	215	125	92	75	63	39	25	14
50	469	269	157	115	93	79	49	31	18
60	563	322	188	138	112	95	59	37	22
70	657	376	219	161	130	111	68	43	25
80	751	430	251	184	149	127	78	50	29
90	845	484	282	207	168	143	88	56	32
100	939	537	313	231	186	159	98	62	36

*t: Average extinction time in generations.

(d) Linked neutral gene model[3/]

In this model a neutral gene is linked with a selective locus. Namkoong and Roberds (In preparation) suggested that when the selective locus has additive gene effect, a good general rule of thumb would be to double the size of the population required when an independent neutral gene model was used. In our example the necessary population size would be 318.

All the gene action types described by the four models are likely to exist simultaneously in a real population. Therefore, the breeder can choose from a large range of population sizes. The size selected will depend on which model is given the most emphasis. A conservative breeder may wish to have a large population size, say 318, to maintain neutral genes in the population for many generations. But this size would be unnecessarily large if model b was given the most emphasis. On the other hand, the breeder could pick 85 as the breeding population size, but this number would be too small for models c and d. Therefore, the choice of population size is subjective.

The application of results obtained from the models is limited, and the population sizes discussed above should not be taken as recommendations. There is no reason why the population size should be 318, 85, etc., and the numbers should be considered as bits of information breeders can use to improve their intuition to breed trees. For example, breeders agree that gene conservation can be achieved by maintaining a large breeding population, but

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[3/] This model was suggested by Dr. Gene Namkoong, and the author is grateful to him for making the information available before its publication.

the definition of "large" ranges from 20 to multi-thousands. The study of models c and d do not generate a fixed number that would define a large population. By studying the models, the breeders can appreciate the fact that the sufficient breeding population size would most likely be in the range of hundreds.

Today, tree breeders are at a crossroad. They have begun to realize that they have to evaluate their breeding systems in respect to time (long-term breeding) as well as space (single-generation breeding). The addition of this new dimension leaves them with a great deal more uncertainties than before. Yet, because experimental means are not available, they have to depend entirely on intuition to develop future breeding population(s). We can improve our intuition by learning the success and failure of crop and animal breeders, and by studying population dynamics.

ACKNOWLEDGMENTS

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TRENDS IN FOREST MANAGEMENT
AS INFLUENCED BY TREE IMPROVEMENT

Bruce J. Zobel[1]

Abstract.--The most immediate effect of tree improvement has been the increased effort in several areas of forest management either to answer questions raised about the best way to take advantage of the improved stock or to develop methodology to accommodate the improved trees that are now being produced. A whole series of tests have been made because of the inclusion of operational tree improvement programs as a part of forest management. For example, some of the best work done on the effect of wood quality on the final product was started to answer questions about the value of changing wood qualities and, even greater, about the effect of shortened rotations yielding high proportions of wide-ringed juvenile wood. Extensive and expensive studies, even to mill-scale proportions, have been made to obtain the information needed.

The effects of including tree improvement in forest management extend through seed handling, nursery operations and silvicultural techniques. Much has been learned relative to obtaining the highest seed yields during extraction and the highest seed-to-plantable seedling ratio in nursery operations. Silvicultural methods related to initial stand density, thinning (including need for precommercial thinning) and especially rotation age are greatly affected by inclusion of faster-growing and better-quality trees. One of the greatest results from application of tree improvement is to enable profitable forestry on what are now marginal sites through production of strains of trees specially adapted to such areas; many companies are now reassessing their concept of what sites are operable and what are not. Development of special strains for marginal sites is making economically operable millions of acres not formerly available.

INTRODUCTION

Forest management practices have changed dramatically in the South during the past 30 years. To a considerable extent the change has been triggered by the inclusion of tree improvement as an integral and operational part of forest management. Direct and indirect pressures resulting from findings or questions raised by tree improvement have resulted in many tests and research activities in the area of forest management. I have said for many years that the indirect effect of tree improvement on forest management is so important that the greatest immediate gain from tree improvement has been the information and activities generated by the search for answers to the questions raised.

A good example of such indirect benefits relates to wood qualities and the properties required for different products, along with the effect of rotation ages on these properties. One of the criteria for a seed orchard in the N. C. State-Industry Tree Improvement Cooperative was to supply wood with specific gravity suitable for the particular product of each organization.

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We obtained a written statement from each member of the Cooperative, signed by a high-level company official, indicating its desires for wood qualities and placed it in our safe as a part of the permanent record of the Cooperative. As a result of this requirement, several organizations which did not know the gravity they desired started some excellent studies on the effects of wood of differing qualities and ages on the desired product; some studies were even made on a mill scale.

The influence of tree improvement has been marked on all phases of forest management. Although somewhat of an oversimplification, the major gains from tree improvement essentially are: (1) shortening the time it takes to produce a given volume of wood, and (2) increasing the quality and size of the stem on which the productive potential of an acre will be "packaged." The tree improver will not radically change the total amount of cellulose produced by a mature stand on a given acre, but he can strongly influence the form and quality of wood produced as well as accelerate the time to grow a given volume of wood using shorter rotations.

Stated alone, the objectives of a tree improvement program seem simple, but their fulfillment is difficult indeed and requires a "marriage" of the improved trees with the best forest management practices available. The need for the complementary genetic and forest management approaches was realized very early and resulted in studies that would otherwise not have been done. For example, no one will argue that good planting stock is not required to get the best return on the investment for intensive site preparation; similarly, the planting of improved trees without the best forest management is a waste of time and effort. Since one of the greatest gains from genetic manipulation of forest trees is the production of the desired tree in a shorter period of time, the need to adjust utilization methods and products for greater volumes of wide-ringed juvenile wood has received a great deal of attention.

STAND DENSITY AND THINNING

The most controversial subject in forest management today is what is the optimum stand density. What constitutes the ideal number of trees per acre is continuously being reviewed and revised. In fact, opinions on the ideal stand density range back and forth like a pendulum.

As faster-growing, better-formed trees become available through tree improvment programs, plantation spacing has been increased, resulting in fewer but larger high value stems per acre. The trend towards wider spacing of a final crop of better quality trees has become rather general on a world-wide basis, although a few organizations still champion very close initial spacing, even to the extent that precommercial thinning is required. Initial close spacing and precommercial thinning to improve stand quality is not necessary when really improved trees are available and wider spaced stands of improved trees can be established to grow to a commercial size before thinning. With initial wide spacing and improved stock, I have seen operations where trees suitable for use as solid products are obtained at the first (and only) thinning.

The attitude relative to plantation stocking throughout the world has historically been towards "too close" spacing, sometimes requiring precommercial thinning. The feeling that "if a few are good, more are better" has been all too widespread. The physiology of tree growth and needs for nutrients and moisture have been overlooked.

With the availability of improved planting stock, the argument that many trees are initially needed to allow sufficient trees of quality at time of harvest, is no longer valid. The genetically improved trees now starting to be harvested in the South are of such a quality as to have a major impact on forest management relative to what are proper stocking levels in plantations.

ROTATION AGE

One of the major objectives of tree improvement is to produce the desired yield and quality crop of trees within a shorter period of time than is possible using "run-of-the-mill" trees. This is being partially achieved at the cost of increasing the proportion of wide-ringed juvenile wood. If this kind of wood is to be efficiently used it will require some change in methods of manufacture and product development. We have been successful in breeding higher density juvenile wood with resultant greater strength but the wider rings still are a problem for which adjustments must be made.

Reducing rotation age is of major economic value. In a recent analysis by Lambeth,[2] the increased profit from an equal percentage improvement in growth rate versus increased yield (carrying capacity) was estimated. Using a certain set of standarized assumptions, he found the following relative profits:

Treatment	Profit Percent
33-year rotation, no improvement	10%
33-year rotation, 10% gain in carrying capacity	21%
30-year rotation, 10% in growth rate only, same volume as 33-year-old unimproved stand	39%

Lambeth shows with this calculation that a 10% gain in growth rate with its shortened rotation age will give nearly twice as much profit as a 10% increase in carrying capacity with no reduction in time to harvest age.

Closely related to stand density is the suitability and need for thinning plantations. There has always been rather violent controversy about which thinning methods are best or whether thinning should even be done. The so-called "row thinning methods" have been under special criticism when they are applied to forest plantations established with unimproved stock. To many of us, row thinning of such stands is really not thinning at all; it is only an early harvest of the stand, resulting in no better trees in the remaining stand than before thinnings, but with the thinned stand now having one-half or two-thirds of the initial stocking. Despite any claims about the value of row thinning resulting from its ability to produce "less expensive wood," the practice has fallen into quite general disfavor except in those stands with ridiculously dense initial stocking because good trees are cut while poor trees are left. As better genetic stock becomes available, resulting in more uniform plantations, some of the adverse reaction to row thinning will have been removed and the main consideration will then be to maintain a suitable level of stocking.

[2] mimeographed report

SEED EXTRACTION AND NURSERY OPERATIONS

Improved seed has high value. Depending on the company and product produced, the value of the extra wood produced from a pound of genetically improved seed at the time of harvest will be worth from $200 to nearly $2000 when discounted to the present. It is an economic necessity that all available seed be extracted and used. This need has resulted in greatly improved seed extraction, storage and testing methods.

Because of the value and scarcity of good seed, every effort must be made to get the highest ratio of seed to seedling and to get the best planting survival possible. As a partial result of this need, seed bed densities in operational nurseries using improved seed have been reduced drastically from as many as 50 or more seedlings/square foot of nursery bed to about 25 seedling/square foot. Positive results in seed-to-seedling ratios and in survival and growth of plantations using improved seed have been dramatic because of the impact of tree improvement needs. Some organizations have even suggested growing their improved seed using special containerization techniques to get better seed-to-seedling ratios and field survival.

GROWING TREES FOR SPECIFIC SITES

A major pressure in southern forestry is the continuing withdrawal of the best forest lands for agricultural and other uses. Consequently, forestry must be increasingly practiced on marginal or submarginal sites. On such sites a profitable forestry enterprise is difficult to obtain if regular trees are used.

Some of the most successful tree breeding involves improved adaptability to marginal sites. As a result, many millions of acres are now being economically forested that were formerly unproductive or wasted. Special strains have been developed for excessively wet and dry sites, developing trees that grow in environments that are colder or more severe than in the species' native range has been especially successful. Large forestry operations in pines and hardwoods are now possible in submarginal environments using valuable species which once were not suited to the area; for example, whole new industries have resulted from growing loblolly pine in parts of Tennessee and West Virginia.

It is now generally recognized by all foresters that provenance (or geographic) seed source is of key importance for successful plantations. Most organizations are very particular not to violate the basic principles of seed movement. In some instances, outside sources have been used in widespread planting to replace indigenous sources because they have proven to grow better or be more resistant or more hardy than the indigenous source.

In a few regeneration programs, the environment of the progeny has been matched with that of the parent from which seed were obtained. One organization plants large total acreages by 50-acre blocks with seedling of different mother trees to better take advantage of the special adaptability and growth and form characteristics of particular genotypes. Such utilization of the genetic potential results in a radical alteration of the forest management techniques used in most operational regeneration programs.

SUMMARY

Forest management practices are currently undergoing dramatic changes. In many instances, these have resulted from, or been initiated by, pressures or needs to better use improved trees obtained from the tree improvement programs. Many sites formerly considered to be nonoperable or submarginal are now being routinely used for economic forest enterprises utilizing improved forest management methods and exploiting the especially developed strains of trees made possible through the use of genetics. Trees with higher value, better form and improved growth rate have resulted in better care from nursery to harvest, with resultant greater returns on the investment.

One major result of applying genetic principles in forestry is the production of trees of a desirable size in a shorter period of time. Although this is very favorable from a total production and return on investment standpoint, it results in a higher proportion of wide-ringed, juvenile wood which the industries must learn to utilize for their products.

As increasing amounts of better genetic stock become available, we can anticipate continued and increasing changes and continued specialization of forest management activities necessary to fully utilize the advantages of the quality trees that are available.

RESPONSE TO NITRATE AND AMMONIUM FERTILIZERS - FLOWERS, CONES AND SEED IN A LOBLOLLY PINE SEED ORCHARD

John F. Robinson[1]

Abstract.--Fertilizer was applied at different rates to two young loblolly pine seed orchards in Louisiana and Texas in the form of nitrate or ammonium nitrogen.

The only response in the Louisiana orchard was to the third year's application when clone x treatment interaction was significant for male and female strobili.

Higher rates were then applied to the Texas orchard. Response to the first year's applications (April and July) showed no difference between the control and the nitrate treatment. The ammonium treatment was greater but significant only at the 10 percent level of probability. Response to the second year's applications showed the nitrogen treatments to be significantly (05 percent) greater than the control but not different from each other. Response was strongly affected by clone.

Seed production was observed and rate of return on investment in dollar value from increased seed crops due to fertilization was calculated at 104 percent and 245 percent respectively for the two years.

Additional keywords: *Pinus taeda*, rate of return

The value of pine seed orchard seed has been estimated at from $100-$1000/pound (Zobel 1974). Whether one assumes the higher or lower figure, such values accentuate the need to manage seed orchards for optimum production.

One widely used and effective technique for stimulating pine seed orchard production is the application of agricultural fertilizer. Nitrogen specifically has been shown to result in yield increases (Anonymous 1971; Schmidtling 1971). Nitrogen usually has been applied in combinations of ammonium and nitrate ions in the form of ammonium nitrate. Some research has indicated that the nitrogen form - ammonium ion or nitrate ion may have an effect on the response of the plant (Pharis *et. al.* 1964; Ebell 1972; Schmidtling 1975). Two experiments were carried out by the Western Gulf Forest Tree Improvement Program (WGFTIP) in cooperation with the Louisiana Forestry Commission and Champion International in their respective seed orchards. The tests were intended to show: (1) if orchards in the western range of southern pines would respond to nitrogen and (2) if there would be a different response to different forms of nitrogen.

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In a preliminary study in one of the Louisiana Forestry Commission's loblolly orchards, 48 pounds per acre of nitrogen was tested over a three year period. Nitrogen was supplied as either sodium nitrate or ammonium phosphate. A complete randomized block design included five replications with five clones each and four treatments. Fertilizer was applied in July and trees were from five to seven-years-old at the time of application. Both phosphorus and potassium were included in the fertilized treatments. Two controls were used, one with and one without P_2O_5 and K_2O amendments.

No female flowering response was observed the first two years. However, flower crops were generally light with large variation among ramets. A significant clone x fertilizer interaction was observed the third year. Some clones responded more to the ammonium form of nitrogen (NH_4) while others responded more to the nitrate form of nitrogen (NO_3). Although the response to NH_4 was greatest, differences among treatment means were not statistically significant. Male flowering was generally very poor. However, one clone responded strongly to the NH_4SO_4 treatment.

With this preliminary information a similar study was initiated in 1974 in Champion International's drought-hardy orchard in southeastern Texas at much higher application rates.

METHODS

A randomized complete block design was used with four replications, six clones, two ramets per clone and three treatments for a total of 144 trees. The same six clones were used in all treatments and replications. Trees to be treated were chosen according to their location in the orchard so that different fertilizer treatments were separated by at least one untreated orchard spot. Trees are spaced 30' x 30' and were four-years-old at time of test initiation. The treatments were:

1. The equivalent of 963 lbs/a of nitrogen and 69 lbs/a of P_2O_5 as $CaNO_3$ and superphosphate broadcast to individual trees in April plus 250 lbs/a of nitrogen applied in July.
2. Same as above except nitrogen applied as NH_4SO_4.
3. Control, no fertilizer applied.

The spring application proved to be too concentrated. Four trees were killed and several showed toxic effects. The nitrate treatments were the most severely damaged. The summer application showed no apparent damage.

In the spring of 1974, before fertilizer application, pollen strobili clusters and female strobili were counted on all sample trees. Flower counts were again taken in 1975. The 1975 flowers were monitored to maturity and in 1976 actual cone and seed yields were observed.

Fertilizer was again applied in April and August 1975 at the rate of 250 lbs/acre of nitrogen either as NH_4SO_4 or $NaNO_3$. One hundred lbs/acre of phosphate was applied in the spring. The 1976 flower crops were observed and followed to cone collection in 1977.

Analyses were made using the Statistical Analysis System (SAS) developed by Barr, Goodnight, Sall and Helwig (1976).

RESULTS

1974 Male and Female

As expected, no significant differences, due to treatment, in male or female flower counts were observed in 1974. These observations were made before fertilizer was applied.

Female Strobili

Figure 1 shows female flowering, with all clones combined, for all three treatments for all three years. Values having different letters are significantly different from each other at the five percent level. In 1975, female flowering in the nitrate treatment was no greater than in the control. The ammonium treated trees showed an increase in flowering which, although not significant at the .05 percent level, indicated a response may be there. In 1976 a large and significant increase in flowering was observed for both fertilized treatments.

Response was strongly affected by clone in both years. In 1976 the two clones which inherently flowered most showed a large increase of flowering in the ammonium treatments. In 1976 with exception of one clone a favorable response was observed in both fertilizer treatments.

It must be noted that the same ramets of the same clones were treated each year, yet response was not the same in 1976 as in 1975. What could account for the difference? Some possibilities are:

a. Fertilizer was applied at a much heavier rate in the spring of 1974 than in later applications.

b. In 1974 nitrate was supplied as calcium nitrate and in 1975 as sodium nitrate (due to unavailability of calcium nitrate in 1975).

c. Rainfall pattern was different. In 1974 spring rainfall was below average through July with exception of one heavy rain in June. In 1975 spring rainfall was well above average through July.

d. There could have been a delayed effect from the initial application.

e. Increased orchard maturity and natural variation of flower crops from year to year. Loblolly pine flowering was heavy throughout the region in 1976.

Male Strobili - 1975 and 1976

Fertilizer treatments also affected male strobili production. In 1975 only two of the six clones had significant numbers of male strobili. Of these, one clone responded slightly favorably to both ammonium and nitrate nitrogen treatments while the other responded negatively to nitrate and very favorably

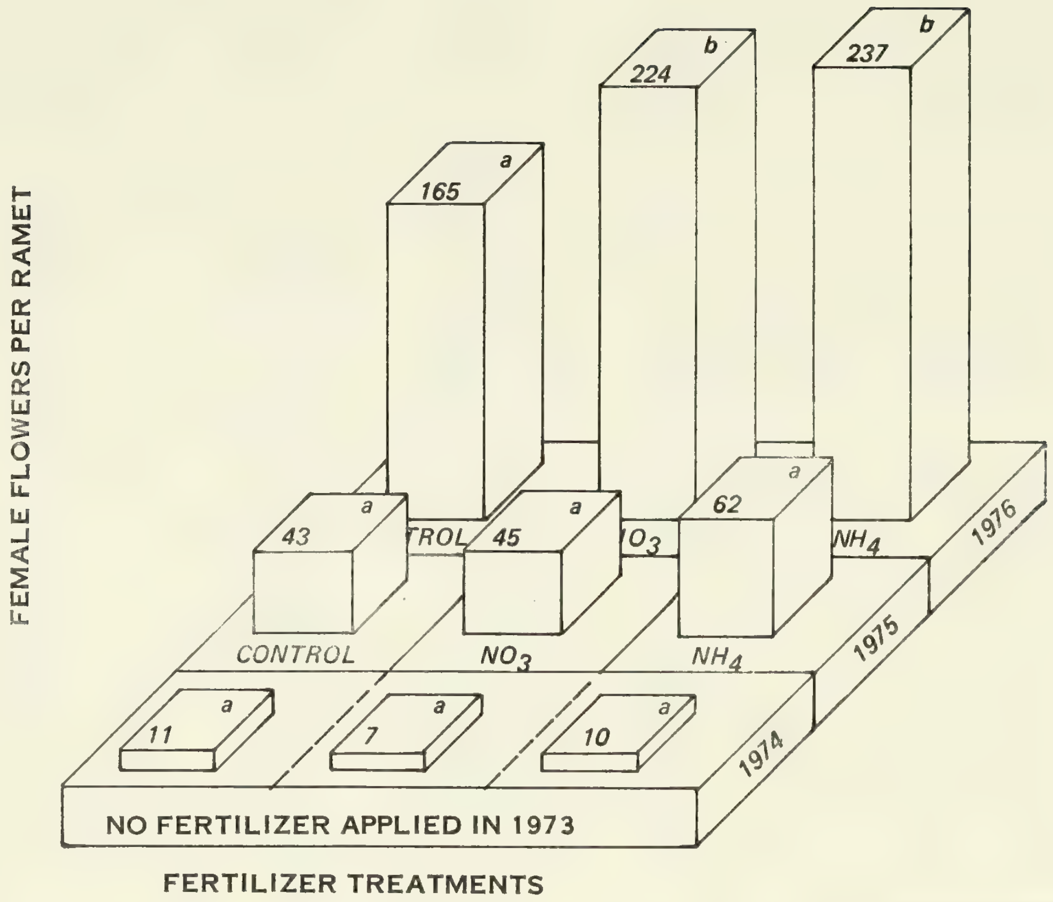

Figure 1. Female flowers per tree by year and fertilizer treatment in young loblolly pine orchard. Values with different letters are significantly different at the 05 percent level of probability.

to ammonium nitrogen. Clone x treatment interaction was highly significant.

In 1976, however, male strobili occurred on five of six clones. Pollen response was generally increased by either source of nitrogen. The exceptions were one clone which showed no response and another which did not produce pollen in any treatment. Male flowering was greatest in the ammonium treatment. Both ammonium and nitrate treatments stimulated catkin production significantly above the control. Clone x treatment interaction was highly significant, however, this was probably due to slope as the response appeared linear with the nitrate treatment intermediate between control and the NH_4 treatment.

Cones and Seed

To determine the economic value of increased seed yield due to fertilization, cone counts and sample seed yields per cone were taken from all trees in this study. The 1976 and 1977 cone and seed crops were measured as these were the crops expected to be affected by the fertilizer applications in 1974 and 1975. As would be expected cone counts per clone were closely correlated with corresponding flower counts 18 months earlier and will not be presented here.

Of more practical interest is the difference in over-all seed yield due to fertilizer treatments. Several variables were observed:

1. Sound cones/tree - The actual number of seed bearing cones collected from each tree. Insect destroyed and empty cones were not included.
2. Sound seed/cone - Up to 20 cones per tree were collected for seed extraction. All seed was extracted by hand. Empty seed were kept separate from sound seed.
3. Sound seed/tree - Sound cones/tree x sound seed/cone.
4. Extractable sound seed/cone - In 1977 commercial extraction was simulated by merely shaking cones for seed extraction before removing all seed. Only filled seed removed in this manner is included in this variable.
5. Extractable sound seed/tree - Extractable sound seed/cone x sound cones/tree.

From Table 1 it can be seen that cone production was greatest in the fertilized treatments for both years. Differences were highly significant in 1977 and very nearly significant in 1976. No significant difference between sources of nitrogen was shown. Ammonium treated trees produced the most cones in 1976 and nitrate treated trees produced most in 1977.

Seed per cone values for both fertilized treatments in both years were consistently higher than for the non-fertilized trees. Significant differences were shown in extractable sound seed per cone in 1977. The greater seed yields from the fertilized trees are shown to result primarily from more cones per tree; however, seed per cone counts on fertilized trees were consistently higher than on unfertilized trees.

Extractable sound seed is used to show the realizable gain in yield that an organization can expect merely from fertilizer application. Total sound seed more nearly reflects the effect of fertilizer application on seed production, even though this total is not all harvested as usable seed.

Table 1.--Cone and seed yields for nitrate, ammonium and non-fertilized loblolly pine in a 6-7 year old orchard. Phosphate was included for fertilized plots.

Variable	Year	Treatment		
		Control	NO_3 + P	NH_4 + P
Sound cones/tree	1976	78	102	122
	1977	203aa**	323bb**	302bb**
Sound seed/cone	1976	67	74	75
	1977	68	78	80
Sound seed/tree	1976	5,628	7,897	9,187
	1977	16,419aa	26,022bb	23,726bb
Extractable sound seed/cone	1977	54a*	67b*	68b*
Extractable sound seed/tree	1977	13,124aa	22,621bb	20,804bb

**Values having a pair of different letters are significantly different from each other at the 01 percent level.

*Values having different letters are significantly different from each other at the 05 percent level.

DISCUSSION

How much is this increased yield worth, and will an investment in fertilizer application in a seed orchard pay off? In order to answer these questions some calculations and assumptions were made. Assumptions to assign values to a pound of seed orchard seed above ordinary seed were:

A. One pound of seed contained 18,000 seed (based on actual samples from this orchard) and is expected to produce 9,000 plantable seedlings. At a planting rate of 750/acre it will plant 12 acres.

B. Stumpage value = $12/cord and $100/MBF Scribner.

C. Interest = 8 percent.

D. Rotation = 30 years (or 31 years from seed).

E. Base growth = 19.2 cords and 7.55 MBF at rotation (Schumacher and Coile 1960).

F. Genetic gain = 10 percent.

The value of a pound of seed orchard seed above ordinary seed is:

$$\begin{aligned} \text{Value} &= \text{Gain}(\text{Stumpage value at age 30})(1 + i)^{-31} \times \text{acres planted.} \\ &= .10\left[(\$12 \times 19.2) + (\$100 \times 7.55)\right](1 + .08)^{-31} \times 12. \\ &= \$109/\text{pound.} \end{aligned}$$

To calculate the increase in value per seed orchard acre achieved from fertilization and the rate of return on investment as shown in Table 2, the following assumptions were made:

A. Number of trees/orchard acre = 40 (30 x 30 foot spacing with 83 percent of positions filled).

B. Cost of fertilizer and application = $125/orchard acre.

Table 2.--Value of increased seed production from application of ammonium or nitrate plus phosphorus in a 6-7 year old loblolly pine orchard.

Variable	Unfertilized 1976	Fertilized[a] 1976	Unfertilized 1977	Fertilized[a] 1977
Sound seed/tree	5,628	8,542	16,419	24,874
lbs sd/tree @ 18,000/lb	0.313	0.474	0.912	1.382
lbs sd/orchard acre @ 40 trees/acre	12.5	19.0	36.5	55.3
Value @ $109 lb[b]	$1438	$2185	$4198	$6360
Value difference/ orchard acre	$747		$2,162	
Estimated cost per acre of fertilizing	$125		$ 125	
Value increase/acre	$622		$2,036	
Rate of Return[c]	104 percent		245 percent	

[a] Fertilized = mean of ammonium and nitrate treatments.

[b] At stumpage value of $12/cd and $100 MBF Scribner, 08% interest, 10% genetic gain, base growth of 7.55 mbf and 19.2 cds/acre at age 30 (S.I. 85).

[c] Rate of return = $\sqrt[2.25]{\text{Return/Cost}} - 1$ (from Davis 1966).

In order to compare fertilized versus unfertilized trees, the means of the ammonium and nitrate treatments were used. Rate of return was calculated by solving the formula, $\text{Cost} = \text{Return}/(1 + i)^n$ for i (Davis 1966). As fertilizer was applied in July to affect the seed crop 27 months later, $n = 2.25$ years.

From table 2 it is readily seen that in both 1976 and 1977, value increases of fertilized over unfertilized trees were substantial. Rates of return on investment were 104 and 245 percent. In 1976 the unfertilized cone crop was average, followed by an excellent crop in 1977. This paralleled the general pattern of cone production throughout the region. Differences in yield attributed to fertilization between 1976 and 1977 probably reflect this yearly variation in cone and seed production. In 1978 cone and seed production was very low and it is doubtful that an application of commercial fertilizer in 1976 would have changed the yield to any appreciable extent. However, even with some years of poor production, the magnitude of gain as illustrated in this six to seven year old orchard indicates how much in dollar value fertilization can mean to an orchard manager.

Results of this study support the use of ammonium nitrate as a source of nitrogen in soil amendments.

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TRICKLE IRRIGATION FOR SEED ORCHARDS

Timothy C. O'Loughlin [1]

Abstract.--Trickle irrigation systems are currently being established in operational seed orchards. Advantages of trickle are efficient water use, improved plant response, logistical improvements in orchard operations, and economies in system design, cost and maintenance. Potential problems of trickle include sensitivity to clogging, salinity buildup, and moisture distribution. Early operation of International Paper Company trickle systems is promising.

Moisture is a critical facet of seed production (Gallegos 1977, Lamb *et al*. 1973, Shoulders 1973, Wenger 1957). Irrigation has been shown to be a successful orchard practice. It can improve survival and growth of young grafts (Long *et al*. 1974); improve crown size and resulting cone production (Davey 1975); and can be used to manipulate the timing of water stress resulting in increased female strobili production (Dewers and Moehring 1970).

These advantages of irrigation have convinced International Paper Company to utilize this technique in its advanced generation seed orchards. Rigorous selection of these orchard sites will allow effective use of water stress to induce female strobili after the initial years of utilizing irrigation to produce large cone bearing surfaces (crowns) on the trees. Use of irrigation and other intensive orchard management techniques allows fewer orchard locations, reduced operating costs, and economies of scale that are essential to a large orchard program. Additionally, the reduced orchard acreage allows for effective management of orchard operations over the long term.

Trickle irrigation was judged better than sprinkler irrigation to meet the orchard requirements of International Paper Company's first advanced generation location - Bellamy II. The water at this location (Marianna, Florida) contained enough calcium that long-term irrigation would raise the soil pH above acceptable levels. This effect has been noticed in a Florida irrigation trial (Schultz *et al*. 1975). The reduced usage and localized placement of irrigation water with a trickle system would help overcome this problem. Additionally, the lower costs of establishing and maintaining a trickle system made it attractive when compared to sprinkler irrigation.

Over 150,000 acres are currently under trickly irrigation in the United States and over 800,000 acres worldwide (Shoji 1977). The first U.S. trickle irrigation system in an operational seed orchard was established by the Texas Forest Service in 1975. Trickle irrigation systems are now in operation in approximately 200 seed orchard acres in the southeast, which includes three International Paper Company seed orchards. More acreage will be irrigated with these kinds of systems in the near future.

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DESCRIPTION OF TRICKLE IRRIGATION

Trickle irrigation can be defined as the supply to plants of filtered water through a low pressure piping system in an exact predetermined pattern that eliminates water spraying or running down furrows and that delivers only a few gallons of water/hour/"emitter." In the soil under each emitter is a "turnip" of moisture (Figure 1) that can be utilized by the tree. The size and shape of the "turnip" is determined by the soil characteristics and the rate and duration of water application. The application of water is on a daily or alternate day basis with trickle irrigation. This frequent irrigation keeps soil moisture tension at low levels when compared to the less frequent water application typical in other systems (Figure 2).

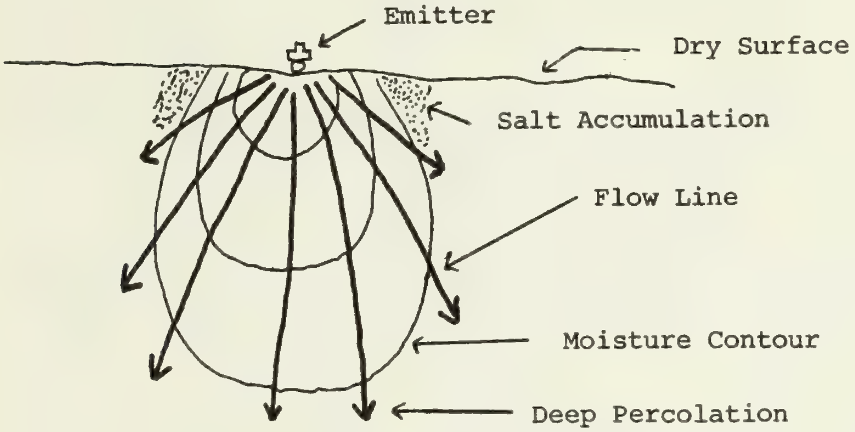

Figure 1
"Turnip" of Moisture

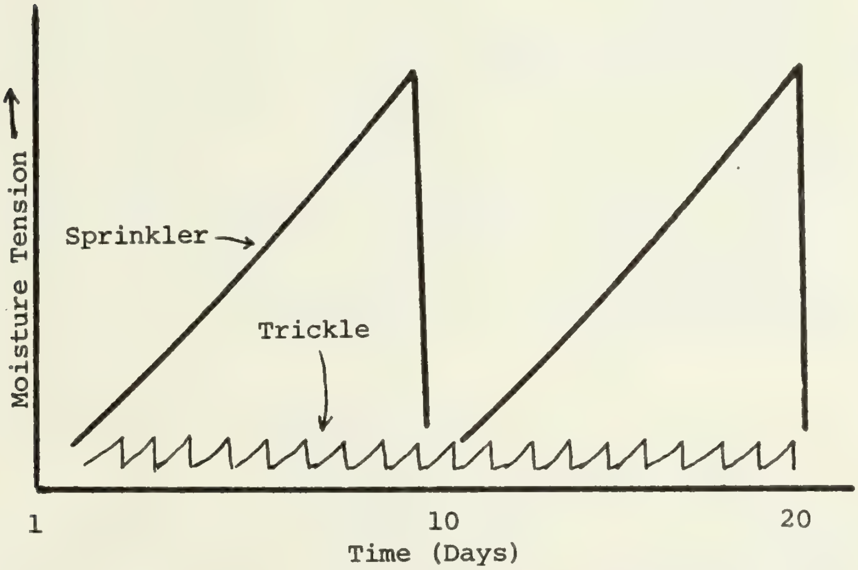

Figure 2
Moisture Tension
Sprinkler vs. Trickle

Trickle irrigation gives only partial ground coverage. For widely spaced tree crops a 20% to 30% coverage is necessary for adequate moisture availability. Table 1 illustrates the coverage that can be obtained with various emitter patterns and soil types (Karmeli and Keller 1975).

Table 1 -- Percentage of Soil Wetted

Spacing between laterals (feet)	Soil Texture Course	Medium	Fine
5	53	80	100
10	26	40	53
15	18	26	36
20	14	20	27

Emitters are located along a lateral to form a continuous wetted soil mass

Emitters. The component about which centers the designing of a trickle system is the emitter. This device is attached to the lateral lines and feeds the water to the soil at flows ranging from 0.5 to 4 gph (gallons per hour). A suitable emitter for an irrigation system should (1) have a uniform and constant water discharge rate, (2) have a large flow cross-section to reduce clogging, and (3) be inexpensive and compact. Many and varied emitters are currently manufactured and each has certain characteristics which affect the design of the system. Emitters can be classified into three types - long path, tortuous path and nozzle - based on the construction of the chamber through which the water flows. Additionally, emitters can be self-flushing and can be designed to compensate for pressure variations in the water supply. The water flow through the emitters can be classified as laminar, partially turbulent, or turbulent. The emitter type, the associated water flow, along with specific construction of the emitter, all affect its overall suitability for a given irrigation application. Careful consideration should be given to emitter selection, particularly to their susceptibility to clogging.

Filtration. Filter requirements are determined by the quality of the water source and the requirements of the particular emitter. Screens of various mesh size are the most common filtration device. Graded gravel and sand filters with back-flushing capabilities can also be used. If large quantities of very fine sand are to be removed, a vortex separator is very efficient. A vortex separator will not remove organic debris and requires another filter (such as a screen), if this is a problem. Settling ponds are an efficient means of removing very large quantities of sand and silt. Filtration of the mineral and organic particles from the water entering the system is of prime importance to the continued serviceability of a trickle system. A trickle system should receive 100% filtered water or no water at all.

Chemical Injection. An irrigation system offers the possibility of applying various chemicals through the system. Many different kinds of equipment are available for these applications. Fertilizers can be applied through a trickle system. Phosphorous is not recommended for application through a trickle system due to problems with its solubility in water, its likelihood of precipitating and clogging emitters, and its immobility in soil. Nitrogen fertilizers generally work well in trickle applications. Anhydrous ammonia and aqua-ammonia generally don't work well due to volatilization of gaseous ammonia and precipitation of soluable calcium and magnesium that may be in the water. Potassium oxide works well in trickle systems. Caution should be used in supplying trace elements through a trickle system due to the low quantities needed, possible reaction with salts in the water and the possibility of excess levels being toxic.

Chlorine (5-10 ppm) can be injected into the trickle system to combat algae growth.

Acid can be injected into the system to remove bicarbonate buildup.

Herbicides can be injected to control weed growth around emitters. Other chemicals may be suitable for irrigation application. Any unfamiliar compound being injected into an irrigation system should first be tested for compatibility with system materials.

Cleaning. Fine sand, silt, and clay tend to settle out in the slow flow at the ends of submains and laterals. Valves or capped ports should be placed at the end of each lateral and along submains to allow the periodic flushing of fine particles from the system.

Hydraulic Design. Careful attention must be paid to producing uniform water pressures in the irrigation system (Kenworthy 1974). An elevation map of the irrigation area should be made prior to installation, although this is not always necessary. Use of pressure regulators, frictional characteristics of pipe, and pressure changes due to elevation, are all important aspects of designing a system that has constant pressure characteristics. Use of pressure compensating emitters simplifies the hydraulic design of a system. Consultation with a knowledgeable trickle irrigation engineer regarding hydraulic design is time and money well spent.

Metering and Monitoring. Keeping account of the amounts of water pumped into various areas is an important control in a trickle system. Due to the discontinuous, visually subtle, nature of trickle irrigation, water applications according to the "look" of an area is very imprecise. Use of moisture-tension measuring devices for the trees and/or soil is a requirement for development of an enlightened irrigation regime.

Level of Automation. Due to the non-visual nature of irrigation through a trickle system, an automatic shut-off should be built into the pump controls. A system that approaches complete automation is possible. The complexity of these systems and their susceptibility to malfunctions argue against a high level of automation. Some level of automation is usually desirable, although a manual system will have fewer breakdowns and the personnel operating the system are likely to quickly discover malfunctions, due to the attention required to operate the system.

PROS AND CONS OF TRICKLE

Advantages. Trickle irrigation has several advantages over conventional irrigation. One is that water use can be reduced by third to half when compared to other systems. Well or reservoir capacity can therefore be considerably decreased. In areas of chronic irrigation water shortage, this can be a considerable advantage. Where water quality is poor, this reduced usage can delay or prevent buildup of undesirable chemicals.

Plant response can be improved by constant low soil moisture tension, elimination of chemical buildup in the soil, and minimizing the beneficial effects of irrigation to competing vegetation.

Logistical improvements are made in orchard operations. The portion of the soil always kept free of irrigation allows unimpeded vehicle operation. A trickle system can be completely underground, thus avoiding any obstructions to orchard traffic. Fertilization is both labor and fertilizer efficient.

Finally, trickle irrigation systems are relatively inexpensive to install, maintain, and operate. Trickle is not adversely affected by the wind, as a sprinkler is.

Disadvantages. When compared with other systems, the major disadvangate of trickle is its sensitivity to clogging the small emitter passageways. Trickle irrigation wets only a portion of the soil volume, and the distribution and coverage of the water must be sufficient to prevent significant moisture stress. In areas where salt buildup can be a problem, trickle systems will buildup a salt accumulation at the fringe of the wet soil mass. A light rain could cause movement of these high salt concentrations into the zone of greatest root activity and damage the trees. This problem can be minimized by operating the system during these rains to leach the salt down through the soil profile. If rainfall is less than ten inches per year, other types of irrigation may be necessary to remove accumulated salts. Due to the thin walls of the tubing commonly used in trickle systems, animal damage can be a problem. Rodents sharpening their teeth or looking for water will cause leaks. Penetration of the emitters through discharge ports by roots can occur.

INTERNATIONAL PAPER COMPANY INSTALLATIONS

Bellamy II. International Paper Company's initial trickle installation is near Marianna, Florida. The size of the installation is 90 acres. A 30 h.p., three-phase electric motor pumps 450 gpm from the Chipola River irrigating 30 acres at a time. Automatic shutoff is provided by a timer. A single manual-flushing 70 mesh screen filters the water, in addition to a large mesh screen on the suction line. Water meter, backflow preventing valves, pressure relief valve and a priming line are included in the pump group. Three different injection points are located on the PVC mainline. The Bermad water-powered injector pump can be used at any of the locations. Eight pressure regulators and gate valves are located between mains and submains. The buried 1/2" PVC lateral can be individually cut off by a gate valve. Flushing of the laterals and submains is possible. Rainbird EM-TB2 emitters are used throughout and provide a 7.5' x 20' spacing. This system has been operational for a year.

Nacogdoches. Another system is approaching completion near Nacogdoches, Texas. This 32-acre orchard is irrigated 16 acres at a time on alternating rows. A double parallel, PVC mainline bisects the sloping orchard and allows for uniform pressures with only a single pressure regulator. A single access point for the Bermad water powered injector is provided. A 7.5 h.p., single-phase electric motor pumps 130 gpm from a settling pond on Black Creek. Automatic shutoff is provided by a timer. Side by side Bermad 150 mesh self-flushing filters, check valves, and water meter complete the pump group. The buried 1"

PE lateral lines can be individually shut off and flushed. Rainbird EM-TB2 emitters are used and form a 7.5' x 30' grid with 2.5 gpm applied through each point. Trees are on a 30' x 30' spacing. A pocket golpher barrier has been placed around the orchard to eliminate damage to the system.

Woodville. A two hectare trickle system has been established near Woodville, Texas. The domestic water well slowly fills a 5000 gallon plastic lined reservoir. A 3 h.p. gasoline motor pumps 40 gpm from the reservoir irrigating the entire two hectares. Automatic shutoff is provided by the motor running empty of fuel. A single back-flow preventing regulator, preceded by a self-flushing 200 mesh filter, controls water pressure entering the PVC submains. A single access point for the water powered injector is provided. The flow of individual laterals is controlled by gate valves. Sixteen different emitter types are installed in this orchard to evaluate their operational reliability. These include the Chapin Micro-dippers; the Dole emitter; Rainbird EM-TB2, EM-TA2, and EM 1010; Spot SRVE, and MRVE; subterrain ST1, ST2, and STF1; Dewline red, and white; Submatic; D.I.I.; and Ein Tal. A flushing capability for the half inch PE laterals and the spacing if 5' x 6' meters. Emitter spacing is variable. The system became operational in 1978.

SUMMARY

Although operational experience is limited, the current trickle systems operate well and no major problems (such as emitter clogging) have developed. Due to the low cost of installation and operation, and favorable initial results, IP plans to install additional trickle irrigation acreage in 1980.

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ROOT DECLINE ASSOCIATED WITH SUBSOILING IN THREE LOBLOLLY PINE SEED ORCHARDS

R. S. Webb and S.A. Alexander[1]

Abstract.--Root systems of 20, 20 and 30 loblolly pines at the Chesapeake Corp., Virginia Division of Forestry (VDF) and Union Camp Corp. seed orchards, respectively, were excavated and analyzed for the impact of subsoiling on healthy and declining trees. The incidence and severity of annosum root rot were also investigated. Colonization of subsoiled root tips by soil-borne microorganisms was recognized by a resin soaked band more than approximately 6mm wide, failure of wound callus formation, and the absence of adventitious root proliferation from tissue proximal to the wound surface. Trees with obvious graft incompatibility, basal fusiform rust cankers or mechanical damage to the bole were excluded. At the Union Camp orchard, both the healthy/subsoiled and declining/subsoiled trees had similar percent numbers of subsoiled primary roots, 76 and 79, respectively. However, the declining/subsoiled trees exhibited much greater primary root resin soaking by length (18%) than healthy/subsoiled trees (8%). At the VDF orchard, declining/subsoiled trees had more subsoiled primary roots (13%) than healthy/subsoiled trees (6%). Primary root resin soaked length was also greater among the declining/subsoiled trees (94%) than healthy/subsoiled trees (82%). At the Chesapeake orchard, declining/subsoiled trees had more subsoiled primary roots (33%) than the healthy/subsoiled trees (18%). However, declining/subsoiled trees exhibited much greater primary root resin soaking (41%) than the healthy/subsoiled trees (0%). Soil texture analysis from the upper 15cm of the A horizon revealed a similarly low percent clay content , 3-7%, for the three orchards. However, the average clay content at a depth of 45cm for the Chesapeake orchard (14%) was much greater than for the Union Camp (8%) and VDF (6%) orchards. The reduced amount of root resin soaking among declining/subsoiled trees at the Chesapeake orchard may be related to this heavier soil texture affording a wetter and thus more favorable edaphic environment for the healing of subsoiler wounds. An experiment will be conducted at the Union Camp orchard this summer to investigate the effects of various available soil moisture levels on root wound healing. Although resin soaking was exhibited in approximately 75% of all subsoiled primary roots, attempts to isolate Heterobasidion annosum were negative. Originally implemented for increased superior seed production, subsoiling may increase root dysfunction and stimulate seed tree decline, especially on droughty sites.

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MANAGEMENT OF AN INDOOR, POTTED LOBLOLLY PINE BREEDING ORCHARD

M. S. Greenwood, C. H. O'Gwynn, and P. G. Wallace[1/]

Abstract.--Since potted, indoor grown grafted ramets of loblolly pine can be made to flower earlier and more profusely than field grown ramets, more rapid completion of second generation breeding plans appears feasible. The management of Weyerhaeuser's potted breeding orchard near Hot Springs, AR is described, including a discussion of the cultural methods, flower stimulation methods and the breeding techniques that are currently being used on indoor grown trees.

Key words: Pinus taeda, early flowering, tree breeding, male and female strobili, gibberellins, water stress, out-of-phase dormancy.

INTRODUCTION

Weyerhaeuser Company is currently committed to shortening the generation turnover time of its loblolly pine breeding program by about 7 years, and is operationally using flower stimulation methods to induce earlier flowering on grafted, young select loblolly pine. The biological constraints on early flowering by loblolly pine have been discussed elsewhere (Dorman and Zobel, 1976, and Greenwood, 1977 and 1978). Young grafts of loblolly pine, even if mature scion wood is used, produce few female strobili and almost no male strobili for several years if they are established in the field.

Over the past several years we have developed a number of flower stimulation procedures which promote flowering on field grown and potted trees. However, our most consistent and effective results have been obtained on potted trees kept in a greenhouse.

WHY AN INDOOR, POTTED BREEDING ORCHARD?

Flower stimulation treatments have been evaluated on loblolly pine cloned by grafting for seed production and/or breeding purposes. The grafted ramets of these clones, ranging in age (from grafting) of from 1 to 4 years, were grown either in the ground in young seed orchards, or in pots both outdoors or in the greenhouse. Scions for these trees came from 4-12 year old select trees in progeny tests, and comprise the parent population for the second generation of our breeding program. The results of a variety of flower stimulation treatments are shown in Table 1, and are further discussed elsewhere (Greenwood, 1977, 1978 and 1979 and Ross and Greenwood, 1979). Operationally we are presently relying on two treatments, which are applications of $GA_{4/7}$ to developing buds on water stressed trees, and out-of-phase dormancy (Greenwood, 1978). While $GA_{4/7}$ has no effect on male flowering, water stress alone in the greenhouse is promotive.

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While good results have been obtained on both field grown and potted trees, we are conducting our advanced generation breeding on indoor grown, potted trees for several major reasons: (1) poor male flowering in response to most of our treatments on small, outdoor grown grafted ramets has been observed (see Table 1). With the exception of wire girdling (Greenwood and Schmidtling, 1979 and Table 1) none of the treatments we tested promoted male flowering outside. However, Hare (1978) has found that GA applications do promote male flowering on 7-8 year old field grown loblolly pine. (2) Female flowering responses by field grown trees are inconsistent (compare the results for Comfort and Magnolia in Table 1), most likely because of variation in rainfall distribution throughout the summer. However, the scion age of the grafts at Comfort is considerably less than those at Magnolia. The average July and August rainfall is twice as great at the Comfort seed orchard as at Magnolia, and the conditions during which these tests were conducted were no exception. In our potted orchards, GA application without water stress during July and August is almost completely ineffective (Greenwood, 1979 and unpublished data), which would explain why GA applications at Comfort had very little effect. (3) Winter damage on potted trees grown outdoors was extensive last winter because of heavy snowfall, and windthrow of the larger potted trees is frequent. The extensive foliar development of the potted trees due to heavy fertilization and the confined root system makes them very unstable outdoors. (4) Out-of-phase dormancy, our most effective flower stimulation treatment for

Table 1. Results of Flower Stimulation Treatments, Potted and Field Grown Trees.

Location	Treatments	% Clones with ♀	% Clones with ♂	Graft Age, Years
Magnolia, AR	GA	100	0	3-4
Seed Orchard	Control	50	0	
Comfort, NC	GA	10	0	3-4
Seed Orchard	Control	5	0	
Hot Springs, AR	GA + WS[1/]	92	54	3
Greenhouse, potted	WS	50	63	
Hot Springs, AR	GA + WS	100	0[2/]	4
Outdoor, potted	WS	60	0[2/]	
Hot Springs, AR	OPD[3/]	80	80	2
Greenhouse, potted	WS	20	0	

[1/] GA = Gibberellin $A_{4/7}$, WS = Water Stress.

[2/] GA treated branches only. Wire girdling resulted in male flowering on 80% of the clones, versus none for the controls.

[3/] OPD = Out-of-Phase Dormancy.

small, young grafts, requires greenhouse culture. This method is particularly useful because of the high frequency of male flowering obtainable after just two years after grafting in the early spring (see Table 1). (5) Breeding in a greenhouse is not hampered by bad weather, and pollen can easily be forced so that the problem of crossing early female strobili with pollen from late shedding males can be lessened in some cases.

MANAGEMENT OF A POTTED BREEDING ORCHARD

Potting Medium. Grafts are made on potted rootstock in 3 gallon pots, usually in the early spring and are kept well watered and fertilized. Summer grafts of soft tissue are also used when more ramets of some clones are required. They are repotted into larger containers in the fall, using a potting medium consisting of 1:1:2:2, (by volume), of peat:vermiculite:coarse quartz sand: hardwood bark. A medium consisting of 2:1:1 (by volume, sand:peatmoss: vermiculite also supports good growth. The high proportion of sand in these media permits good drainage and allows prompt buildup of water stress.

Fertilization. Essential elements are supplied by application of Osmocote^{R} (9 month formulation, 18-6-12 analysis Sierra Chemical Co., 1001 Yosemite Dr., Milpitas, CA 95035), first by mixing directly into the potting medium at 6 g/l, and later by top dressing with 2-3 g/l of Osmocote^{R} as recommended by the manufacturer. In mid summer, the trees are top dressed with ammonium nitrate at a rate of about .8 g/l of pot volume. Trace elements can be added occasionally in the form of Peter's Fritted Trace Elements^{R} (R. B. Peters Co., 2833 Pennsylvania St., Allentown, PA 18104), but are probably not necessary when hardwood bark is used.

Table 2. Scion Elongation by 1975 Grafts in 68 1 Pots from 6/10/75 to 1/5/76. Two ramets each of 4 clones were included in each treatment.

	Fertilizer	Application Frequency	Rate	Scion Length		Scion Diameter	
1	5x Hoagland's Solution	1x per week	15 ml/l	145 cm	bc[1/]	22 mm	ab
2	9 mo. (18-6-12) Osmocote	1x per 9 mo.	1.3 g/l	174 cm	a	25 mm	a
3	3 mo. (18-9-3) Osmocote	1x per 3 mo.	.7 g/l	162 cm	ab	25 mm	a
4	Fertilizer mix[2/]	1x per mo.	.4 g/l	134 cm	c	19 mm	b

[1/] Similar letters indicate no difference between treatments.

[2/] 9:3:4 Urea:Superphosphate:KCL by volume.

We have compared the effects of four fertilization regimes over 1 growing season on grafted trees during the first season after grafting. Scion length and diameter after 1 growing season are shown in Table 2. The nine month osmocote treatment significantly promoted scion elongation compared with the Hoagland's solution or fertilizer mix. There was no significant difference between the response to the two osomocote formulations, but the three month formulation significantly outperformed the fertilizer mix. There was little difference among levels of foliar nutrients between all 4 regimes, although potassium was about 30-50% higher with our fertilizer mix. Soil pH was between 4.1 and 4.6 for all treatments. In our opinion the 9 month osmocote formulation is the regime of choice because it was the most stimulatory for vegetative growth and it is the most convenient treatment to apply. There was not sufficient flowering by the grafts used in this experiment after one year to evaluate the effect of the four fertilizer regimes on flowering, but there were no obvious differences. All the potted trees referred to in Table 1 were fertilized with Osmocote, and all have flowered very well.

Watering. Watering of the potted orchard is done automatically, using a "Spaghetti" watering system which consists of 1½" diameter PVC laterals, with each tree served by leader tubing connected to an irrigation ring or turret in each pot (see Stuppy's Greenhouse Supply Co., 1212 Clay St., North Kansas City, MO 64116). Watering of an entire block can be accomplished by simply turning a valve or using a timer controlled solenoid.

The watering regime during the initiation and differentiation of strobili is probably the single most critical phase of the management of a potted breeding orchard. Failure to provide the right intensity and duration of water stress can result in a considerable reduction of the flower crop. Water stress is applied from June through September, and begins after a considerable amount of vegetative growth has occurred. Stress is monitored by means of irrometers^R and a pressure bomb, and the regime followed depends on the size of the tree, and whether or not cones are already present on the tree.

Insect Control. Control of tip moth and seed and cone insects is carried out by yearly application of the systemic insecticide Disyston^R 15 g in late February, at a rate of .2 g/l, applied to the soil surface. DeBarr (personal communication, 1978) recommended Furadan 10 g^R at rates as high as .6 g/l, but suggested that several rates be tested. In 1978, we have tried applications of .2 and .5 g/l in late February and have noted no phytotoxicity symptoms at either rate. This year, we are trying rates as high as 1 g/l, and have not as yet seen any phytotoxicity clearly attributable to Furadan. The 1979 cone crop will represent the first real test of the effectiveness of these insecticides on protecting cones from insects.

Flower Stimulation and Breeding. Based on the flowering performance in response to the flower stimulation treatments that we have observed, breeding should be complete about 5 years after the selections have been grafted. This period would allow three breeding seasons, during which male and/or female strobili could be expected on almost all the clones involved. At present, our breeding plan is based on a six parent disconnected half diallel, with no relatedness tolerated between the parents within the diallel. A total of 15 crosses are made within each diallel, so each clone must be a male or female parent 2.5 times on the average, but 5 times at the maximum. Ideally, good pollen producers with few females can therefore act exclusively as pollen parents, and *vice versa*. In practice, however, the most efficient use of available strobili dictates some reciprocal mating, assuming that maternal effects are inconsequential. Assuming that 500 filled seed are required per cross, and that 50% of the females will survive and produce 30 seed/cone, then a total of 33 female conelets are required per cross, or 83 per 2.5 crosses. Over a 3 year period 1 ramet should produce about 44 conelets on the average, so a minimum of *2* ramets per clone will be needed.

CONCLUSION

While we have only been managing our indoor potted breeding orchard for a short time, the abundance of both male and female strobili on young grafts has resulted in pollination of over 1400 female strobili included in 4 diallels over the past two years. While we do not as yet have much data on seed yield per cone, preliminary results indicate that we may be able to expect at least 30 seeds per cone. At present, breeding loblolly pine indoors appears feasible.

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RELATIVE GEOGRAPHIC STABILITY OF RESISTANCE TO FUSIFORM RUST OF SELECTED SLASH PINE FAMILIES

R. E. Goddard and R. A. Schmidt[1]

Abstract--Open pollinated progenies of 45 slash pine families which exhibited fusiform rust resistance in previous tests and four known rust susceptible families were established in nine potentially high rust incidence tests from Mississippi to Florida and Georgia. Rust frequency (percent of trees within a family with at least one rust gall) three years after planting was used to evaluate disease resistance.

Among locations average rust frequency varied from 11 to 64% for resistant families and from 15 to 82% for susceptible families. Significant variation in rust frequency was evident at each location, but discrimination of resistance among families increased as the mean rust frequency of the test increased. Some families exhibited high rust resistance in all locations although the family x location interaction was significant. Some of the most resistant families contributed greatly to this interaction as their relative disease frequency was lowest in high rust incidence locations. Of the 49 families tested, 25 possess very desirable levels of resistance over a large geographic area.

Additional keywords: Genetic variation, *Pinus elliottii*, *Cronartium fusiforme*, pest management, epidemiology.

The incidence, distribution and impact of fusiform rust, caused by *Cronartium fusiforme* Hedgc. & Hunt ex Cumm. have increased dramatically in much of the planted slash pine ecosystem since 1960 (Schmidt et al. 1974; Griggs and Schmidt, 1977; Dinus, 1974; Powers et al., 1974). Starting in 1969, increased emphasis was placed on genetic improvement of rust resistance by the University of Florida Cooperative Forest Genetics Program.

Although there is little or no evidence of pronounced provenance variation in rust resistance in slash pine (Snyder et al. 1967), early studies (Arnold and Goddard, 1965; Barber 1961; Jewell, 1961) indicated that rust resistant individuals existed throughout the species range and that this resistance was inherited. Preliminary analyses of artificial inoculation with *C. fusiforme* (Goddard and Schmidt, 1971) and general field progeny tests (Schmidt and Goddard, 1971) of previously selected families in the program indicated that: 1) population means in rust frequency did not differ between selected families and bulk lots; 2) some select families were resistant; 3) field progeny tests with low rust incidence were not useful to differentiate resistant and susceptible families.

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Consequently all families (approximately 1200) were screened for rust resistance through both artificial and natural inoculation. Artificial inoculationswere initially conducted at Gainesville and later at the USFS screening facility at Bent Creek, N.C. Natural inoculations were accomplished by establishing special progeny tests in high rust incidence areas (Sohn, Goddard and Schmidt, 1975). Families with potential rust resistance, as judged by their performance in one or all of the inoculations described, were established in nine progeny tests specially designed to further evaluate their rust resistance.

METHODS AND MATERIALS

Using preliminary data from one or more of the previously described screening procedures, open pollinated seed of potentially resistant families and susceptible check families were sown in the nursery in April, 1974. Resulting seedlings were distributed in January, 1975 to cooperators for establishment in nine specially selected rust hazardous locations in Florida, Georgia and Mississippi (Figure 1). At each location 10-tree row plots of each family were planted in five randomized blocks.

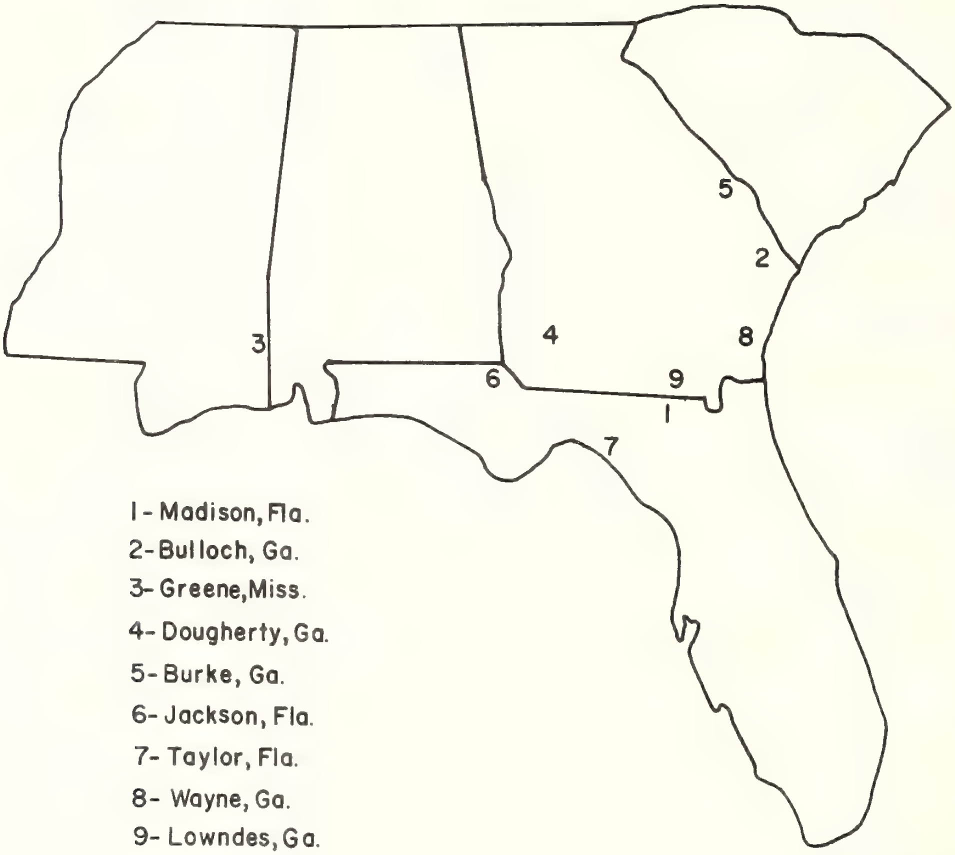

Fig. 1. Test locations on rust hazardous sites.

Rust frequency data (percent of trees in each plot with at least one rust gall) were recorded in January 1978, three years after planting. Family plot means (% rust) were analyzed since previous analyses (Sohn, 1977) indicated that these unadjusted data were sufficient to differentiate family resistance.

A separate analysis of variance was completed for each of the nine locations. Two combined analyses of variance: 1) 49 families common to three locations and 2) 24 families common to 8 locations provided estimates of the host geneotype x location interactions. In addition, regression analyses of individual family performance in the various locations were used to examine the nature of host genotype x location interactions.

RESULTS

Average rust frequencies for those families common to at least four locations are presented in Table 1. Location means varied from 11 to 64% for "resistant" families and 15 to 82% for susceptible check families. Family means varied from 19 to 56% for "resistant" families and from 44 to 58% for susceptible families. Within locations, individual family means varied from 0 to 94%.

Significant variation among families was evident at each location and differentiation of relative rust resistance among families as indicated by the F ratio, increased as the mean rust frequenc of the test (location) increased (Figure 2).

Combined analysis of 24 families common to eight locations and 49 families common to three locations (Table 2) indicated that there were significant differences among locations and families and that significant interactions between families and locations occurred.

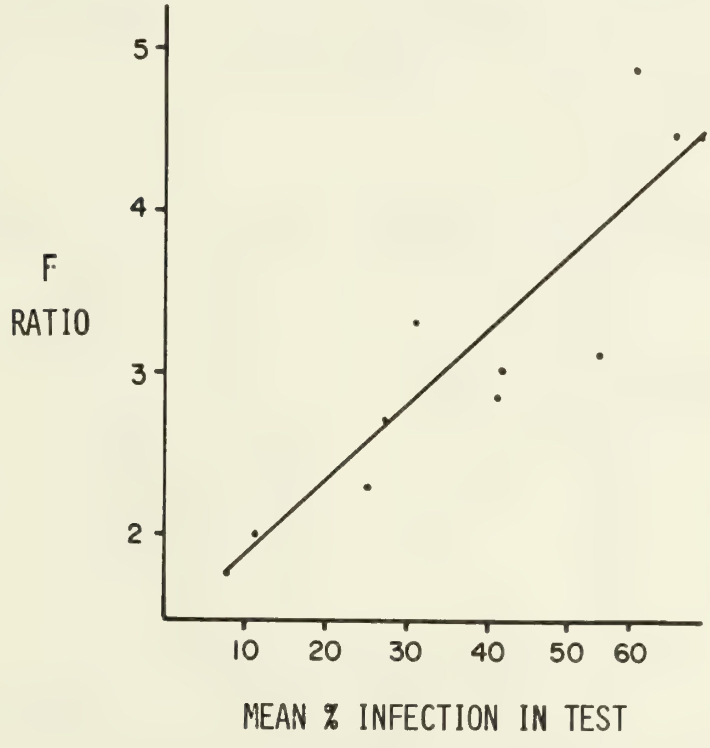

Fig. 2. The relationship between mean fusiform rust frequency and the F ratio (infection variance among families/error variance) for 9 progeny tests.

Table 1. Mean fusiform rust frequency of slash pine families established in nine locations.

	Location #[1]									
Family #	1	2	3	4	5	6	7	8	9	Mean
potentially resistant					%[2]					
6-56	13	0	14	38	57	25	33	15	41	26
C-129	27	25	7	27	40	29	24	10	39	25
B-210	17	20	9	42	62	29	30	26	36	30
119-56	20	22	13	40	57	40	34	30	63	35
79-56	25	45	11	31	48	38	35	36	64	37
257-56	22	23	23	49	60	47	41	21	62	39
246-55	26	27	6	48	66	39	36	25	64	37
123-61	23	17	10	64	67	33	36	14	80	38
7-56	25	26	10	61	56	45	41	24	67	39
286-56	34	41	14	55	61	36	33	22	57	39
B-617	32	33	7	69	77	31	51	26	54	42
M-724	48	30	8	72	60	47	51	29	58	45
215-56	34	26	8	55	70	34	54	12	74	41
261-56	45	21	12	64	61	37	42	25	44	39
164-58	25	15	10	70	68	61	46	28	85	45
310-56	28	39	4	56	82	60	37	29	66	45
27-58	38	26	15	58	57	42	58	36	58	43
451-55	46	32	9	69	87	60	54	46	87	54
62-56	32	32	8	74	84	56	55	56	92	54
110-56	62	40	8	72	74	65	55	26	86	54
311-56	37	43	18	77	72	56	56	24	94	53
316-56	24	6	16	29	45	19	9	14		20
28-60	20	9	4	39	31	23	27	16		21
179-55	19	19	6	43	30	23	23	20		23
16-59	25	16	14	54	35	48	18	13		28
187-57	22	28	20	50	62	58	40	22		34
186-57	48	48	24	80	94	77	40	31		55
165-57	10	13	4	39	58	29	41			28
205-55	23	16	6	51	38	39	16			27
57-57	22	29	13	38	45	41	35			32
293-55	23	22	0	59	42	37	41			32
106-56	16	18	10	64	67	39	47			37
74-61	57	28	32	55	77	50	52			50
C-135	20	2	2	33	29	29				19
70-56	19	13	4	34	41	22				22
89-57	23	16	5	34	32	26				23
163-57	33	31	16	39	48	34				34
C-67	32	13	12	37	29	27				25
52-56	14	21	0	44	77					31
315-56	36	41	10	57	78					44
B-629	37	23	12	50						31
240-57	32	25	15	47						30
189-57	26	29	10	58						31
33-58	48	17	4	52						30
298-56	61	50	29	85						56
Mean	30	26	11	52	58	40	40	25	64	
susceptible										
262-55	33	29	9	81	92	70	69	50	78	57
121-56	57	64	12	67	84	48	65	35	90	58
30-62	49	38	29	80	84	67				58
UC	31	20	12	78	70	45	42	21	75	44
Mean	42	38	15	77	82	58	59	35	78	54
Test mean	31	27	11	54	60	42	41	26	66	40

Table 2. Analysis of variance of fusiform rust frequency of selected slash pine families.

Source of variation	49 families in 3 locations		24 families in 8 locations	
	Degrees of Freedom	Mean Square	Degrees of Freedom	Mean Square
Locations	2	57287**	7	34041**
Blocks (Locations)	12	892	32	417
Families	48	2063**	23	4172**
Loc. x Fam.	96	388*	161	383*
Fam. x Blocks (Loc.)	576	320	725	304

*, ** = Significant at 0.05 and 0.01 confidence levels, respectively.

Partitioning of the total family x location variance among the eight locations with 24 common families (Table 3) showed that this variance was not equally distributed among locations. Interaction variance appeared to be distributed in relation to neither the amount of rust nor geographic pattern.

Table 3. Fusiform rust frequency family x location interaction variance distribution among test locations.

Location	Fam. x Loc. % of Variance[1/]	Mean Rust Frequency %
Madison, FL	15.4	31
Bulloch, GA	19.9	27
Dougherty, GA	15.1	54
Burke, GA	8.3	60
Jackson, FL	9.3	42
Taylor, FL	6.2	41
Wayne, GA	13.1	26
Lowndes, GA	14.1	66

[1/] Proportions of variance per location were calculated from analysis of 24 families at 8 locations.

Partitioning the total family x location interaction variance among the 49 families common to three locations indicated that the interaction variance was not equally distributed among families. Family 79-56 accounted for 12% of the total interaction variance although, if the variance were distributed equally among families, each would have approximately 2%. Two of the susceptible check families accounted for a relatively high proportion of the interaction variance. Several resistant families showed little interaction. Family 6-56 accounted for only 0.17% of the interaction variance, or in other words, performed relatively the same at each location, always among the least infected families.

Relative consistency of performance is shown by regression of family means on test means (Fig. 3). For example, the rust frequency of family 6-56 closely paralleled average infection at each location, increasing as the test mean increased. In contrast, the rust frequency of C-129 was little lower than the test average in locations with low or moderate general infection but had substantially lower infection than average in locations with high mean frequency. C-129 was associated with a much larger portion of the family x location interaction. Very low and high contributions to interaction are illustrated by families 28-60 and 79-56. It is evident that 79-56 did not perform with high consistency in the various locations.

The 25 families with the lowest average rust frequency are listed in Table 4 along with results of regressions of the infection of these families on test means. Note that for all but two of the families, the correlation coefficient is significant, indicating that in most cases, infection of individual families is related to general incidence level at each location. Of particular interest is the slope of the regression. Slope values higher than 1.0 indicate a relative lower resistance in locations with high rust incidence. However, only three of the listed families have slopes greater than one and 14 have slopes indicating

Table 4. Regression of fusiform rust frequency per test of 25 rust resistant slash pine families on mean frequency per location.

Family	r[1]	slope[2]	Family	r	slope
C-129	.86*	.55	16-59	.74*	.74
6-56	.85*	.83	187-57	.89*	.95
B-210	.84*	.73	205-55	.85*	.82
119-56	.95*	.88	165-57	.93*	1.09
79-56	.75*	.63	57-57	.92*	.63
246-55	.98*	1.07	283-55	.92*	1.04
257-56	.94*	.88	C-135	.88*	.68
286-56	.92*	.82	70-56	.99*	.74
261-56	.83*	.81	89-57	.97*	.57
361-56	.69	.54	C-67	.77	.44
28-60	.93*	.67	163-57	.95*	.55
179-55	.88*	.58	240-57	.99*	.75
			B-629	.96*	.90

[1] Correlation coefficient. * = significant at 0.05 confidence level.

[2] Percent increase in frequency with each 1.0% increase in test mean.

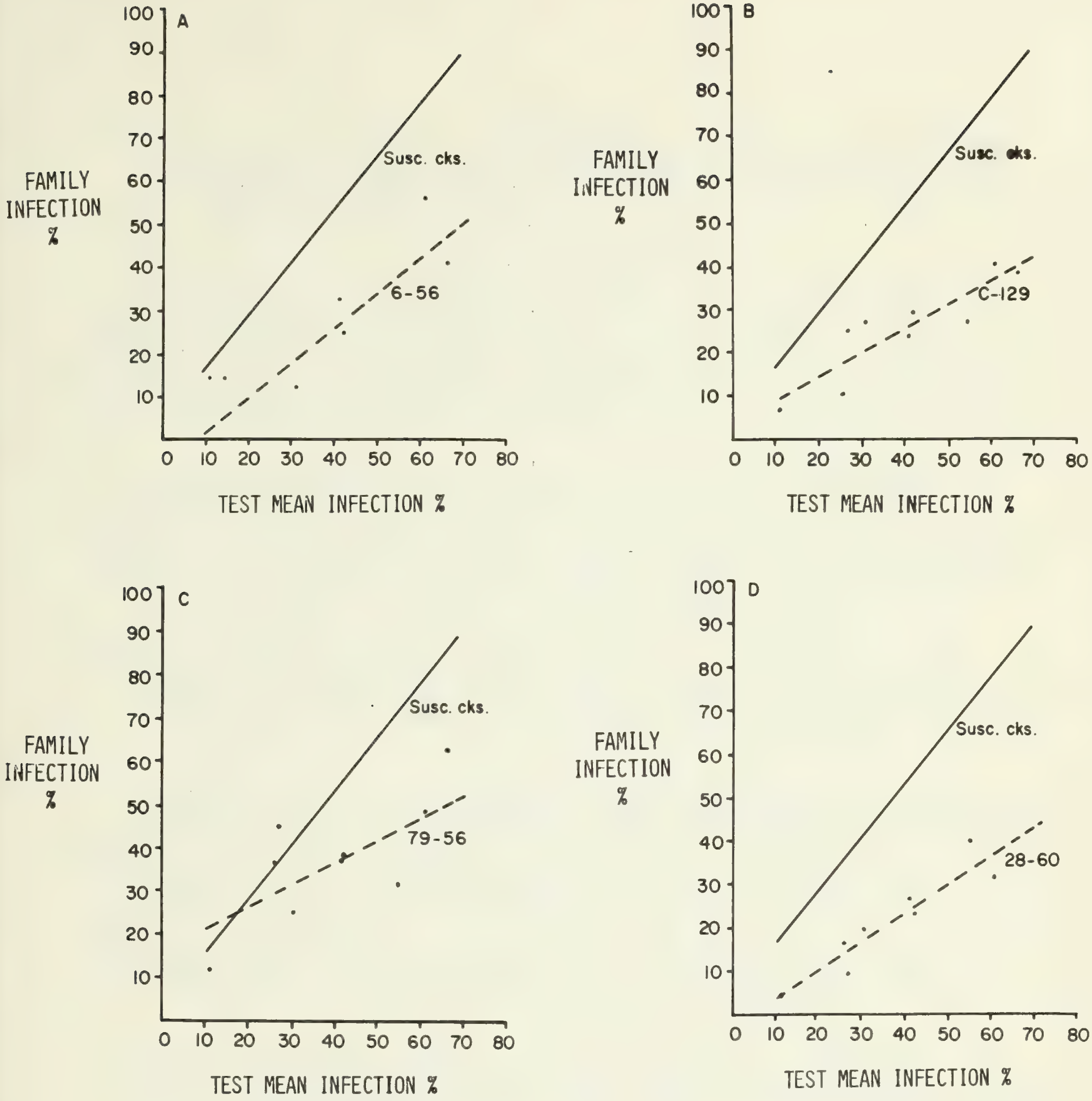

Fig. 3. Regression of individual slash pine family fusiform rust frequencies on test mean frequencies at 9 locations: A. Family frequency nearly parallel to test mean frequency. B. Increase in family frequency approximately 1/2 that of test mean increase. C. High family x location interaction. D. Low family x location interaction.

increase in frequency with increasing incidence at a rate less than 75% that of the average. Note also that the two families with lower than significant correlations with test means increase in infection at about half the normal rate.

DISCUSSION AND CONCLUSIONS

The trees established in this series of tests (with the exception of Test 3) were exposed to substantial amounts of natural fusiform rust inoculum although this is not fully evident from test means. Rust exposure is better indicated by the rust frequency of the susceptible check lots which ranged up to 92% and averaged 59%, omitting Test 3. Average frequency in families selected as resistant was consistently below that of the susceptible lots and this was particularly true for the 25 most resistant families.

However, the preliminary screening for resistance completed at the time choices were made for inclusion in these tests did not eliminate all susceptible families. At least 10 of the "resistant" families were as frequently infected as the control lots. It appears that limited simple tests will not thoroughly and reliably discriminate relative rust resistance in all cases.

With a few exceptions, the family x location interaction does not appear to be a serious problem. In fact, the interaction caused by increasing expression of resistance at higher disease incidence levels is beneficial. This type of performance shown by 14 of the families is more indicative of their relative resistance than their overall mean infection.

Data from these tests indicate little promise for fitting families with resistance to narrowly defined geographic locations. There was, for example, as much difference in relative ranking of families in Bullock and Burke County, Georgia tests which are in close geographic proximity as there was among rankings in tests more widely separated. The development of different rust resistant orchards for each specific location is not practical and the inclusion of clones in such an orchard which are resistant over a wide area seems more promising. However, the single test location in Mississippi in the western portion of the species range and the low exposure to rust inoculum in this location precludes conclusion that an East-West interaction does not exist.

Of the 45 families tested in 5 or more locations, 25 families showed very useful levels of resistance and 15 appear to be highly resistant in all eastern locations. Some families demonstrated stability of resistance over the entire geographic scope of the series of tests and, in so far as fusiform rust is concerned, would be useful for planting over the entire area. No implication of stability of resistance over time is implied by these tests. However, for the present, slash pine families such as these can provide substantial reductions in fusiform rust incidence on sites suitable for planting slash pine.

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EARLY GROWTH OF PLANTED NORTHERN RED OAK AS INFLUENCED BY GENOTYPE AND NITROGEN FERTILIZATION

by

R. E. Farmer, Jr.[1]

Abstract--Twenty open-pollinated families of 1-0 seedlings were grown for five years on a well-drained, alluvial site after applying 360 kg/hectare of nitrogen during the first and second years after planting. Mean five-year height of individual families ranged from 2 to 3 meters, and was on the average 47 percent greater than unfertilized controls. After deletion of treatment variance, 16-percent of remaining variance in height was associated with family differences, while the family x fertilization interaction was not significant until the fifth year when it accounted for 8 percent of variance. The genetic correlation between five-year heights in controls and the fertilization treatment, another measure of genotype x environment interaction, had a coefficient of 0.67. Larger trees had both greater numbers of shoot elongation flushes per season and larger individual flushes than poor performers.

Additional keywords: Genotype x fertilization interaction, shoot growth components.

Growth of planted northern red oak (*Quercus rubra* L.) has been stimulated by nitrogen fertilization (Foster and Farmer 1970, Gall and Taft 1973) which shows promise of being a beneficial establishment practice. Looking beyond this general response, however, it will be important to use planting stock which has especially good response to nitrogen since fertilization interaction research is stock with excellent potential for both early growth and reponse to nitrogen.

METHODS

One-year-old bare-rooted northern red oak seedlings from 20 open-pollinated southern Appalachian parent trees were lifted in March 1973. Twelve replicates of 4-tree family subplots were planted at 1.2 x 1.2 m spacing in an abandoned nursery area, which had been treated with Dalapon to kill grasses, then plowed and disced. The planting was divided into three blocks of four treatment plots, each of which received one of the following treatments:

(1) Control
(2) Irrigation
(3) Fertilization
(4) Fertilization and irrigation

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The design was thus a split-plot with treatments as main plots and families as subplots.

The irrigation treatment consisted of supplementing natural rainfall in July and August of 1973 and 1974, when soil moisture deficits might have limited growth. An irrigation hose was attached to the nursery irrigation system and plots were thoroughly soaked at biweekly intervals. Ammonium nitrate (1000 kg/hectare) was broadcast on fertilization plots on May 4, 1973, and again in mid-April 1974. During the 1973 and 1974 growing season, the test area was cultivated as necessary to keep it free of weeds. In 1975, the area was cultivated once; it was not cultivated in 1976 or 1977.

Total height of each tree was recorded at planting and after each growing season from 1973 through 1977. Each year's height growth was also recorded as number and length of individual flushes of main shoot elongation.

In August 1974, leaf samples (without petioles) were taken from three trees in each plot and ovendried for 24 hours. After grinding to 60 mesh in a Wiley mill, samples were analyzed for nitrogen, phosphorus, potassium, calcium, and magnesium. The semimicro-Kjeldahl procedure was used for N, the molybdovanadate test for P, and atomic absorption spectroscopy for Ca, K, and Mg.

RESULTS

Analyses of variance in total height revealed significant family differences throughout the test period and significant treatment differences starting with the second growing season. Irrigation had no effect on growth in either the first or second years and was discontinued after the second year. The degree of height response to fertilization (Figure 1) ranged from 28 percent over controls after the second growing season to 47 percent over controls at the end of the test. The range of family means around treatment means was broad throughout the test; at five years it was slightly over 1 m for the fertilized trees, which has a mean of 2.5 m. There was, however, no significant fertilizer x family interaction until the fifth year. Since some family differences in height were present at planting, a correlation analysis of family means at planting with those at five years was computed. The resulting correlation coefficient of 0.41 indicated that major changes in family rankings took place during the course of the test.

Variance components for families and the family x treatment interaction were computed using the model below with data from the fifth year measurement. Within-plot variance was computed using data from every tenth plot.

Source of Variation	Expected Mean Square	Variance Component	Percent of Variance
Families	$\frac{\nabla^2 w}{K} + \nabla_R^2 + RT\nabla_F^2$	527	16
Treatment x Families	$\frac{\nabla^2 w}{K} + \nabla_R^2 + R\nabla_{TF}^2$	256	8
Error II	$\frac{\nabla^2 w}{K} + \nabla_R^2$	±0	0
Within Plot	$\frac{\nabla^2 w}{K}$	2,466	76

Separate analyses of variance were also computed for control and fertilized plots with the following results:

		Control		Fertilization	
Source of Variation	Expected Mean Square	Variance Component	Percent Variance	Variance Component	Percent Variance
Families	$\frac{\nabla^2_w}{K} + \nabla^2_R + R\nabla^2_F$	376	14	534	17
Replication x Families	$\frac{\nabla^2_w}{K} + \nabla^2_R$	±0	0	±0	0
Within Plot	$\frac{\nabla^2_w}{K}$	2,250	86	2,599	83

Together these analyses indicate that around 16 percent of the total variance unrelated to fertilizer effects was associated with family differences, and that the degree of genetic variation was roughly the same under both control and fertilizer treatment.

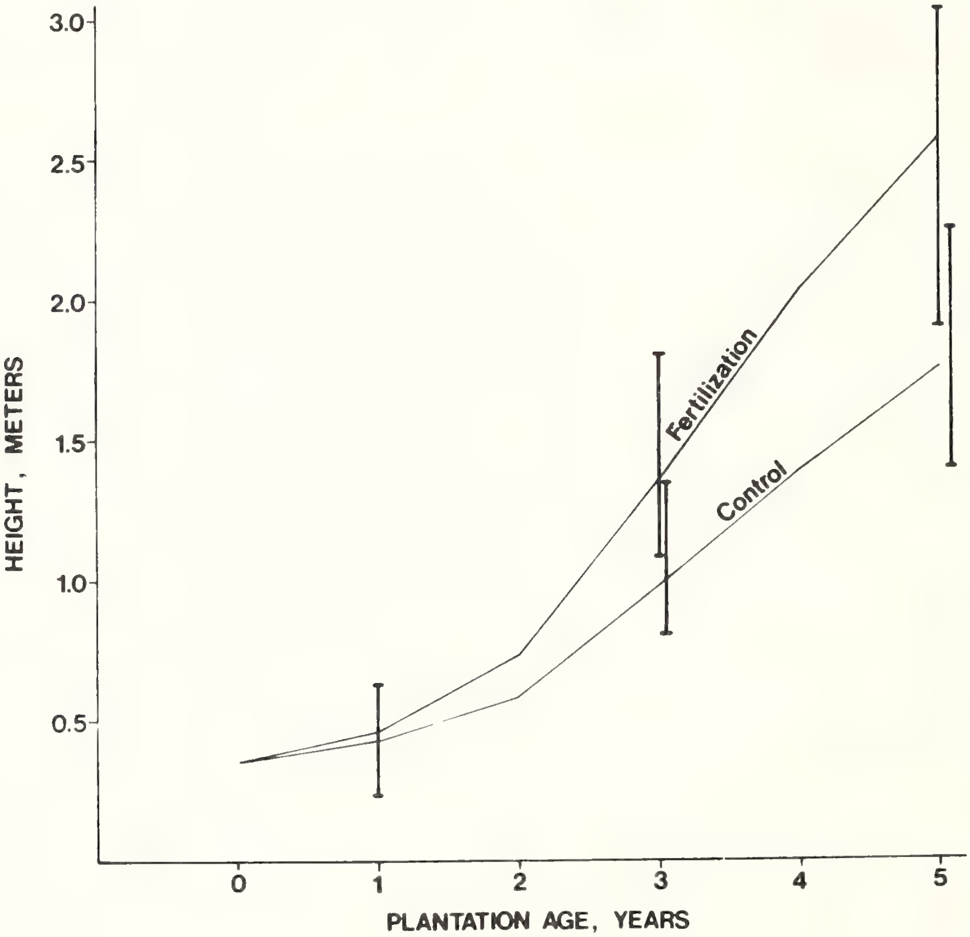

Figure 1. Effect of nitrogen fertilization on height of planted northern red oak. Vertical bars indicate range of family means in control and fertilization treatments.

The family (genotype) x fertilizer interaction accounted for approximately 8 percent of the variance. Family means for fifth year height in the fertilization treatment ranged from 18 to 89 percent over equivalent means in controls. Effect of fertilization upon the relative performance of families was also examined by correlation analysis, as suggested by Burton (1977). The correlation of family means for fifth year height in the control and in fertilization treatment had a coefficient of 0.67; the rank correlation coefficient was 0.33. The genetic correlation between these two sets of heights also had a coefficient of 0.67. Thus, less than 50 percent of the family variation in height in the fertilization treatment was associated with family differences in controls. Correlation analysis of family means in controls vs percentage response produced a correlation coefficient of -0.56, indicating that the slower growing families in controls tended to respond slightly better to fertilization than the control families with the higher rate.

Differences in height growth due to fertilization and family effects were examined in terms of shoot growth components. Shoot length of individual plants in a species with episodic elongation patterns, such as Quercus, is related to at least two components: (1) number of elongation flushes and (2) the spatial length of flushes. Data for the second, third, and fourth seasons are presented in Table 1. Fertilization resulted in a greater number of flushes in all three seasons, and the number of flushes per season decreased with plant age. In all years a higher precentage of fertilized plants made second, third, and fourth flushes than did control plants. Plants which made the greatest number of flushes also had greater flush length throughout the season. These same components were examined for several fertilized families with small and large heights at five years, and the same pattern (Table 1) was apparent. Height differences are positively related to both number and length of flushes. Number of flushes decreased and the length of individual flushes increased with age.

Foliar analyses indicated that K, P, Ca, and Mg were at normal levels and were not affected by treatment. Fertilization increased nitrogen levels from 2.33 to 2.54 percent. The base levels of nitrogen were higher than those noted in studies by Phares (1971a, b) and Mitchell and Chandler (1939), whose work suggests that both levels in this test were adequate for good growth.

DISCUSSION

In this test, nitrogen fertilization increased growth of planted seedlings on a site where foliar analysis of control trees suggested no major nitrogen deficiency. The percentage growth response (with control as basis) was substantially less on the average than the 70 percent increase observed by Foster and Farmer (1970) in a test where two applications of ammonium nitrate were supplemented by commercial fertilizer (15-15-15). However, some families exhibited a response equal to that in the previous test. Total growth and general response to fertilization were both greater than that noted by Buckner and Maki (1977) for northern red oak on an old field in eastern Tennessee.

The conclusion stemming from these tests is that nitrogen amendment, as well as weed control, will be essential to rapid dominance by oak on

Table 1. Flushing characteristics of northern red oak trees having variable height growth due to fertilization treatment or genotype.

Item	Season	Mean Number of Flushes	Percent of Trees Making Flush Number				Mean Length of Flush Number				Basis
			1	2	3	4	1	2	3	4	N
Control, all families	2	2.1 ± 1.0[1]	100	68	30	10	7	11	17	21	60
	3	1.8 ± .9	100	60	12	0	26	22	21		60
	4	1.3 ± .5	100	27	3	0	35	21	14[2]		60
Fertilization, all families	2	2.4 ± .8	100	83	48	5	9	14	22	26	65
	3	2.4 ± .6	100	100	52	2	34	28	37	52[2]	66
	4	1.8 ± .6	100	67	13	0	45	36	23		63
Family #715, fertilization $\overline{M}$ height, 206 cm	2	1.9 ± .8	100	58	26	0	6	8	20		19
	3	2.0 ± .6	100	84	16	0	27	21	31		19
	4	1.4 ± .5	100	37	0	0	39	29			19
Family #876, fertilization $\overline{M}$ height, 320 cm	2	2.9 ± .9	100	91	73	41	9	10	23	23	22
	3	2.2 ± .6	100	91	27	0	34	39	32		22
	4	1.6 ± .6	100	50	5	0	51	37	20[2]		22

[1] Standard deviation

[2] Based on 1 or 2 plants only

suitable old field sites where there is competition mainly from herbaceous vegetation. Moreover, it is likely that this amendment will be more beneficial, in terms of total growth on the best sites and that irrigation is unlikely to be valuable during establishment, at least under southern Appalachian conditions. Other research (Buckley and Farmer 1974) suggests that differences established during the first several years will persist.

There was wide variation among open-pollinated families under both control and fertilization. During the first few years, this variation was not significantly influenced by nitrogen amendment, but by five years when the establishment phase was completed, a genotype x fertilizer interaction accounted for substantial variance. Due to this interaction and the associated low correlation between family means in the two treatments, selection in one regime will not necessarily provide the best materials for the other. For example, at five years the top two families in controls were also the top two under fertilization, but a family ranking 16th in a field of 20 in controls ranked 3rd in the nitrogen treatment.

Data on the basis of differences in shoot growth (due to either genotype or fertilization) are of both fundamental and practical significance in that they (1) provide information on the way in which oak grows and (2) may offer keys to effective early selection of superior genotypes or evaluation of growth-stimulating treatments. This test indicates that good early performers can be expected to have both a greater number of flushes and larger individual flushes. Three to four flushes are common on good performers during the first year or two, but number of flushes rapidly declines during ontogeny until about the fifth year, when one long flush is probably typical of most plants. Gall and Taft (1973) noted that nitrogen amendment applied during the fourth growing season changed the number of flushes from one to two during that season. The reduction in number of flushes per season with ontogeny has been considered by Borchert (1976) as a function of the tree's increasing complexity and more specifically as the effect of rapid leaf area development on secondary shoots. If such a relationship does in fact control primary shoot elongation, pruning of lower branches (in stands such as those of this test) should promote height growth during the period of crown closure immediately after establishment (5-6 years).

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PROGRESS REPORT: IMPROVED SEEDLING PRODUCTION IN THE SOUTH

Clark W. Lantz [1]

Abstract.--Production of genetically improved seedlings in the 13 southeastern states in 1977-8 totaled 370 million or 41% of the 895 million seedlings grown. Improved seedlings amounted to 38% of the state nursery production, (45% of the industrial nursery production,) and (39% of the federal nursery production.)

INTRODUCTION

In almost 30 years of active tree improvement work in the South, we can be proud of many accomplishments. We have three active tree improvement cooperatives which include eight southern state forestry organizations, 36 forest industries and one forest seed company. The other five southern state forestry organizations all have independent tree improvement programs, most of which have cooperative arrangements with universities or U. S. Forest Service research projects. In addition, the southern region of the U. S. Forest Service and TVA both have active tree improvement programs.

There are more than 9,000 acres of seed orchards established in the South. These orchards produced over 60 tons of pine seed in 1977. Six of these orchards have produced more than 100 pounds of seed per acre including one loblolly orchard (Weyerhaeuser - North Carolina) which averaged 197 pounds per acre over the entire 33 acre orchard.

NURSERY PRODUCTION

Overall nursery production in the South has increased from 857 million seedlings in 1975-6 to 877 million in 1977-8 (figure 1). In 1975-6, state nurseries produced 54% of the total southern production while in 1977-8, state nurseries produced 55% of this total.

Reforestation personnel in the 13 southeastern area states (AL, AR, FL, GA, KY, LA, MS, NC, OK, SC, TN, TX, and VA) predict that the 1979-80 seedling crop will total 599 million (figure 1). If the 29 southern industrial nurseries continue to produce 391 million seedlings, the total will be 990 million for this season. However, heavy rains this spring washed out seedbeds in some nurseries and cool weather delayed germination in others. For these reasons this season's production may not reach the prediction of 990 million seedlings.

New industrial nurseries in Alabama, Arkansas, Mississippi, South Carolina, and Texas will make a significant impact on the overall reforestation effort in the South. A total of 8 nurseries are in various stages of construction, including one (Champion - South Carolina) which started in production this spring. Since about 44% of the state nursery production is contract-grown seedlings for industry, the completion of these new industrial nurseries should free a substantial production area within the state nurseries. Hopefully, this will enable some state nurseries to establish better crop rotation schedules and improved soil management procedures.

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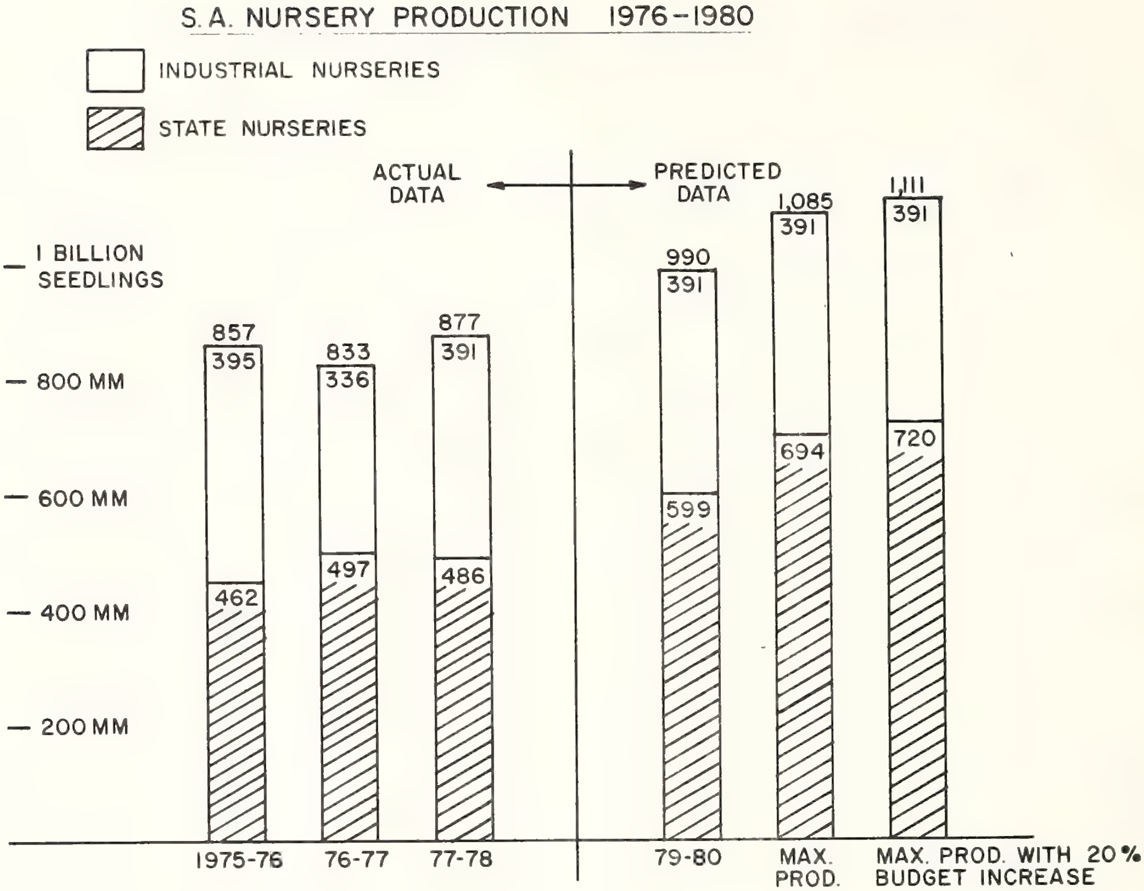

Figure 1.--Nursery production in the South: 1975-1980.

IMPROVED SEEDLING PRODUCTION

The number of genetically improved seedlings produced in the state, company, and federal nurseries in the South has steadily increased in the past three years from 27% in 1975 to 41% in 1977-8 (table 1, figure 2).

State nurseries have made the most dramatic improvement by increasing the percentage of improved seedlings from 14 in 1975-6 to 38 in 1977-8. It is predicted that the 1979-80 state nursery crop will be 43% improved seedlings. Industrial nurseries increased the number of improved seedlings from 41 to 45% in the 1975-8 period, while the Ashe nursery percentage increased from 35 to 39%.

With one exception, all the southeastern state nurseries produced some improved seedlings in the 1977-8 season (figure 3). State nurseries in Alabama, Georgia, Louisiana, North Carolina, South Carolina, Texas and Virginia produced substantial numbers of improved seedlings in that season. The three states with the highest percentage of improved seedlings were Georgia (80%), South Carolina (73%), and Texas (59%).

Table 1.--Improved seedling production in the South (millions of seedlings)

	1975-6	1976-7	1977-8
State nursery production (total):	462	497	486
Nursery-run:	398	379	300
Improved:	63	118	186
% Improved:	14	24	38
Industrial nursery production (total):	395	336	391
Nursery-run:	232	176	214
Improved:	163	160	177
% Improved:	41	48	45
Federal nursery production (total):	20	21	18
Nursery-run:	13	10	11
Improved:	7	11	7
% Improved:	35	52	39
Total production:	877	854	895
Nursery-run:	643	565	525
Improved:	233	289	370
% Improved:	27	34	41

Company nurseries in Alabama, Florida, Georgia, North Carolina and Virginia produced substantial numbers of improved seedlings during 1977-8. The highest percentages of improved seedlings were produced by company nurseries in Florida (85%), North Carolina (81%) and Alabama (76%).

HOW CAN WE MAXIMIZE THE GAINS FROM IMPROVED SEEDLINGS?

In order to develop the full potential of these improved seedlings, nursery management techniques need to be improved. Emphasis must be placed on quality rather than quantity.

1. Soil management procedures must be updated (Leaf 1976). New sources of organic matter must be found to replace depleted stocks of sawdust and bark. Composting of sewage sludge with wood residues is a promising technique which is currently under evaluation at several nurseries. Fish sludge and MILORGANITE are being used sucessfully at the USFS Wind River nursery (Dutton 1979).

2. Precision seed sowing is essential in order to better utilize improved seed and to enable mechanized pruning of lateral roots. Low seedbed densities (20-25 seedlings per square foot) are necessary to enable adequate diameter growth and root development.

3. New species of mycorrhizae indicate a great potential for improving both nursery and field performance of pines and hardwoods (Cordell, et al 1979; Kormanik, et al 1977).

4. New herbicides are more effective and cheaper than the chemicals used in the past (South 1979).

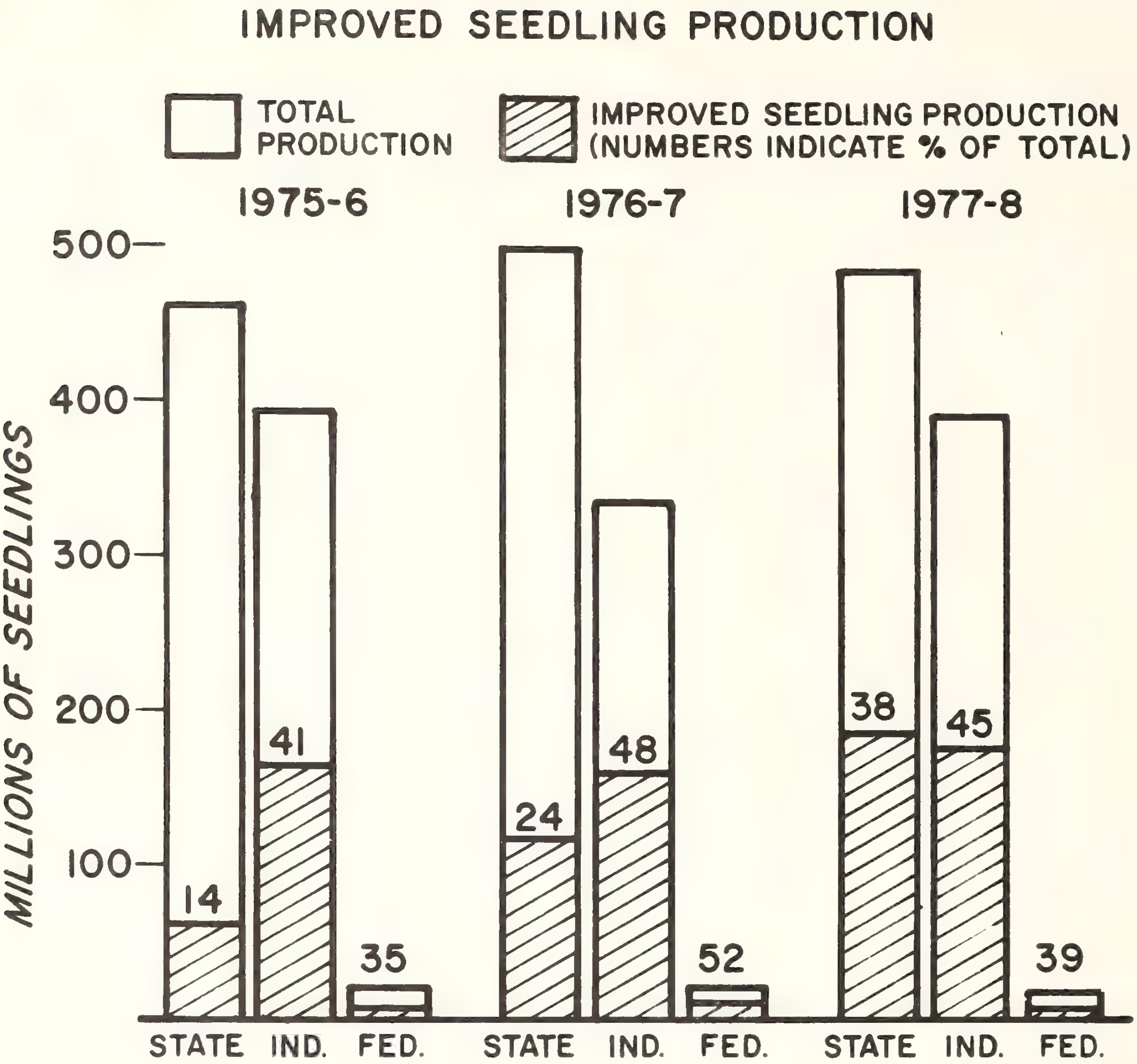

Figure 2.--Improved seedlings from southeastern state, industry and federal nurseries.

5. Root wrenching has been an effective means of encouraging compact, dense root systems of Pinus caribaea and P. radiata in New Zealand (Bacon and Hawkins 1979). Use of this technique in this country, in the Pacific Northwest and the South resulted in variable degrees of success. New evaluation studies are underway by both federal and industrial research groups.

6. Top pruning has been used by several nurseries to restrict top growth, add diameter growth and encourage root growth through the fall (Dierauf 1977).

7. A well-planned schedule of withholding nutrients and water in the fall will also slow down active top growth and promote earlier dormancy.

8. Careful adjustment and operation of mechanical lifting equipment will minimize damage to the seedlings. The optimum survival and growth of seedlings is dependent on undamaged root systems and intact mycorrhizae.

9. There seems to be a popular belief that seedlings packed in Kraft/Polyethylene bags can be treated like pulpwood! Nothing is farther from the truth. The K/P bags were developed specifically for cold storage use. Seedlings confined in the bags will produce considerable heat just in the process of respiration. When temperatures rise inside the bags, fermentation can take place very quickly.

Recent studies in the Pacific Northwest[1] have indicated the importance of good air circulation in cold storage units. The internal temperatures of K/P bags without good air circulation were as much as 22°F higher than those with good air circulation. Merely piling bags more than two deep on pallets resulted in a 10°F increase in temperature. These increased in temperature where bagged seedlings were maintained in cold storage, point out the potential for rapid temperature increases when seedlings are packed in K/P bags and taken out of cold storage. Bagged seedlings left in the sun for just a few minutes can build up lethal temperatures. The entire process of tree breeding, improved seed production and high quality seedling production in the nursery is a complete waste of time and money if the seedlings do not survive! Careful inspection and constant supervision of the storage, shipping and planting operations are essential for the realization of maximum genetic gains from the overall tree improvement process.

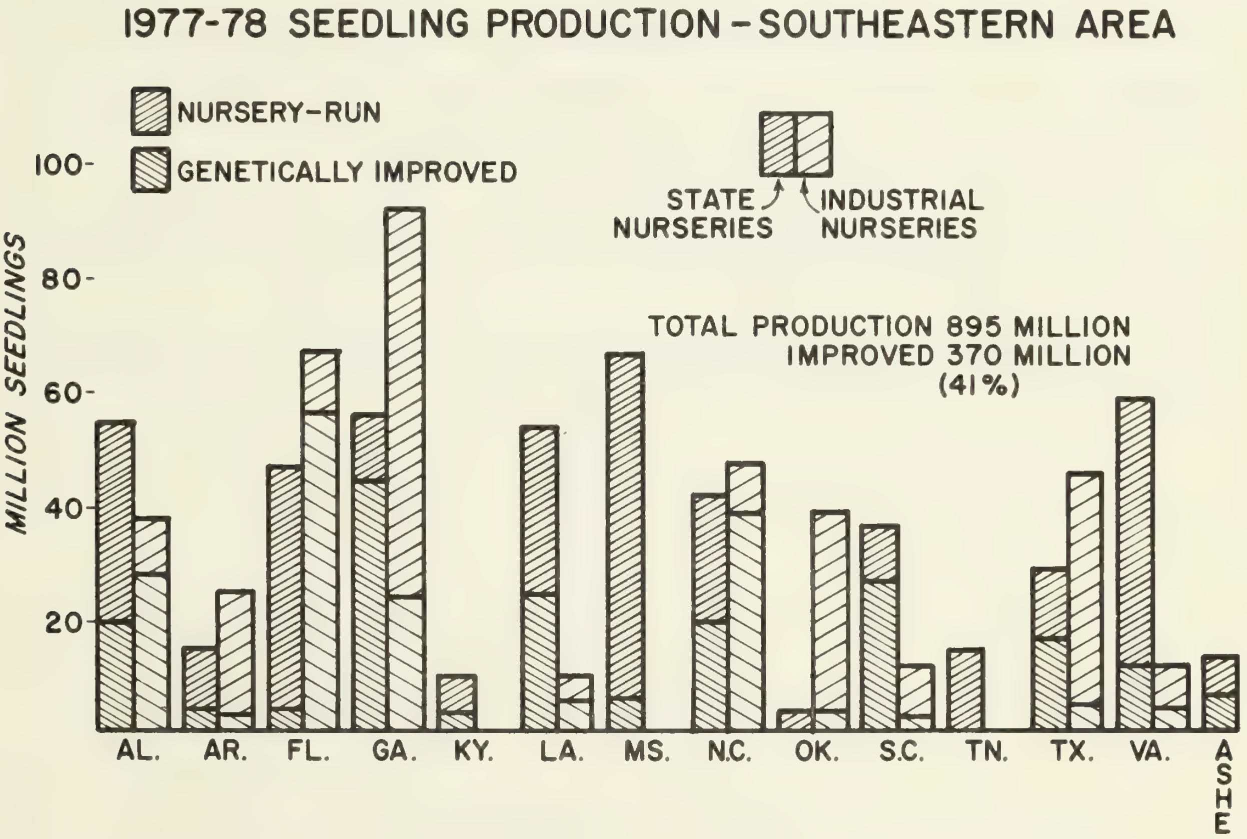

Figure 3.--Improved seedling production: 1977-8.

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[1] Personal communication from P. J. Heide, Scott Paper Company, Hamilton, WA.

SUMMARY

Genetically improved seedlings currently amount to 41% of the 895 million seedlings grown in the South. Many southern seed orchards are producing commercial quantities of seed with a total production of over 60 tons of pine seed produced in 1977. Maximum genetic gains from this improved seed will be accomplished only if major improvements in nursery technology and seedling handling can be implemented.

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SOUTHERN TREE IMPROVEMENT'S IMPACT ON FOREST PRODUCTS - THOUGHTS ON THE FUTURE

Richard L. Porterfield[1]

Abstract.--Past findings with respect to the economic value of tree improvement work are reviewed. These previous findings indicate that tree improvement activities have been economically worthwhile. Recent trends in product prices and the value of quality characteristics, however, promise to move profitability even higher. Because the forest products industry faces unprecedented demand, the tree improvement specialist has never been in a better position to contribute to southern forestry.

Nearly all economic evaluations of southern pine tree improvement programs have shown them to be economically worthwhile investments (Dutrow, 1974). In fact, most studies (for example early work by Davis (1967)) have demonstrated that volume gains of less than five percent justify tree improvement work. So why have this discussion of the economic value of tree improvement? It is simply because the economic setting within which the tree improvement specialist works is not static, but rather ever-changing. There have been and are some very significant changes taking place which should impact tree improvement efforts. Following a short review of past findings, this discussion will focus on the influence that economic trends may (should) have on the economic merits of tree improvement work.

PREVIOUS FINDINGS

I wish I could report that there have been several recent economic studies evaluating tree improvement activities, but to my knowledge there has not been. Such studies are needed to improve upon available results.

In 1973, I did a detailed study of first generation clonal seed orchards and cited the following major findings (Porterfield, 1973):

1. The economic return from tree improvement activities is high. Internal rates of return of 10 to 14 percent are common for most programs. Accounting for a real price rise in stumpage value raises the rate of return to above 16 percent. These results are considered conservative.

2. Total volume gain from first generation clonal seed orchards ranges from 12 to 14 percent over unimproved plantations. In addition, a 5 percent improvement in specific gravity is predicted if this trait is being selected. Straightness and crown improvements for existing programs are in excess of 5 percent for each organization studied and a 10 percent reduction in volume lost to fusiform, in areas of medium infection, is easily attainable.

3. The expensive progeny testing phase and subsequent roguing of the orchard is an economic practice. In fact, the model indicated that roguing intensity should be increased toward the biological limit if maximum economic return is the principle objective. Volume gain could be doubled or tripled with a strategy of putting more clones in the orchard at a close spacing and then utilizing a higher roguing intensity.

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4. Results clearly demonstrated the merits of speciality orchards with a limited number of clones. Candidate traits might be disease resistance, high specific gravity or others. Given likely heritability, selection for fusiform resistance is quite profitable in medium to high fusiform rust incidence areas.

5. Costs associated with the selection of superior individuals in wild-stands or, currently, in plantations seem high, but actually more should be spent. For first generation orchards, wild-stand selection expenditure should have been tripled in order to realize maximum economic worth from tree improvement. These selections effectively determine initial genetic gain.

6. Similarly, while actual orchard seed production is more than sufficient to guarantee high profitability, there is a direct and proportional relationship between seed production and profitability in an existing orchard. Within the orchard, genetic gain is largely fixed. This means the insect and disease control in the orchard and overall orchard maintenance are of the utmost importance. Allowing a 20 percent loss in seed yield means a 20 percent decline in that year's net present value from tree improvement.

7. It is imperative that organizational goals for tree improvement be established early. There are opportunities to tailor tree improvement programs to an individual organization's goals during the selection process, but only if goals are known. Conversely, without firm initial goals significant errors can be made and the tree improvement program not meet its potential.

8. Given two traits, A and B, with a positive genetic correlation, it can be most cost effective to select for gain in A through its correlation with trait B. For example, bole straightness and desired crown characteristics had a genetic correlation of 0.65 in the study (Porterfield, 1973) and greater gain in straightness per dollar spent on wild-stand selection was often obtained by selecting for improved crown characteristics. Thus, if trait A were phenotypically apparent, it could be selected for in order to achieve gain in a highly positively related trait, B, (which might not be phenotypically apparent) with little loss in genetic efficiency and a gain in economic efficiency.

AN UPDATE

What events have occurred since 1973 that have significant impact on the above findings? First, the value of wood raw material has gone up appreciably. An increase in stumpage value is a mixed blessing for forest industry since it makes controlled wood more valuable, but also raises the price of outside wood. This increase in value, at least for sawtimber sized material, has included an increase above the general inflation rate (a real price rise) and this typically signifies a tightening supply situation.

The major impact of this rapid escalation of stumpage value is to make tree improvement work more profitable. Costs associated with first generation orchards are sunk, i.e. can not change, but the revenues are increasing. The 1973 conclusion that first generation orchards had internal rates of return from 10 to 14 percent was based on some $12 per cord for pulpwood and only $40 per MBF for sawtimber. Recent stumpage prices should increase the rate of return from tree improvement to between 15 and 20 percent.

A second economic trend that influences the economics of tree improvement work is the change in relative prices of finished southern pine products. Representative prices for random length 2 x 10 #2 (top) and 2 x 4 #2 (middle) southern pine lumber (per MBF) and for a thousand square feet of standard ½ in. exterior southern pine plywood are shown in Figure 1.

Considering only the lumber price lines, it is obvious that the premium for wide boards is growing. The differential, 10 in. vs. 4 in. deminsional lumber increased from $8 per thousand in 1971 to $35 per thousand in 1978. The compound rates of growth are provided on the figure. The point is that the quality aspects of the resource are of growing importance. The likelihood of obtaining 10 in. lumber from future plantations is dependent on growth rate certainly, but bole straightness will be of increasing value for the size of material likely to be harvested.

Previous estimates of the value of tree improvement work have been based on volume growth only. Characteristics such as crown form and straightness were valued only through their genetic correlations with volume growth in the results cited above. The economic value of quality improvement may well be rising at a faster rate than that for volume improvement.

The bottom line in Figure 1, plywood, has the most rapid rate of growth. This fact goes a long way in explaining the tremendous past and present growth of the southern pine plywood industry. Observation of veneer yield as plywood blocks are peeled is convincing with respect to the importance of traits such as limb size and straightness. Since the south's principle plywood product is sheathing, these quality characteristics combined with growth rate will determine whether a proper ratio, C vs. D face veneer, is maintained.

Concurrent with increases in recent product prices, costs, particularly those associated with heavy equipment, have risen rapidly. From 1967 until 1976 the wholesale price index (now producers price index) increased 70 percent while the wholesale price index for southern pine lumber increased some 110 percent. Cost of mechanical site preparation however increased well over 200 percent (Moak, 1977). The importance of planting seedlings with a 15 percent or so volume gain capability is obvious. Returns must be increased to maintain acceptable profitability.

Cost of mechanized thinning is also up dramatically. The greater uniformity associated with improved plantations should be of great aid in this instance (Davis, 1971). Mechanized thinning is a "slave" to extremes today. With greater uniformity in stand diameter, equipment can be designed to better fit specific site/stand conditions. This uniformity, particularly in specific gravity, should also improve processing (especially cooking time) in the pulp and paper industry.

Overall, recent trends have significantly increased the profitability of tree improvement work both because of rising raw material values and the growing importance of quality characteristics. Remember, too, that many of the costs associated with tree improvement have occurred in the past and that any actions to add to genetic gain or seed yield are probably good marginal investments. For this reason, the importance of maximizing improved seed yield has never been greater and those with sufficient improved seed may consider means of increasing genetic gain. Could more roguing be done in the

Figure 1. Price Trends for Various Southern Pine Products

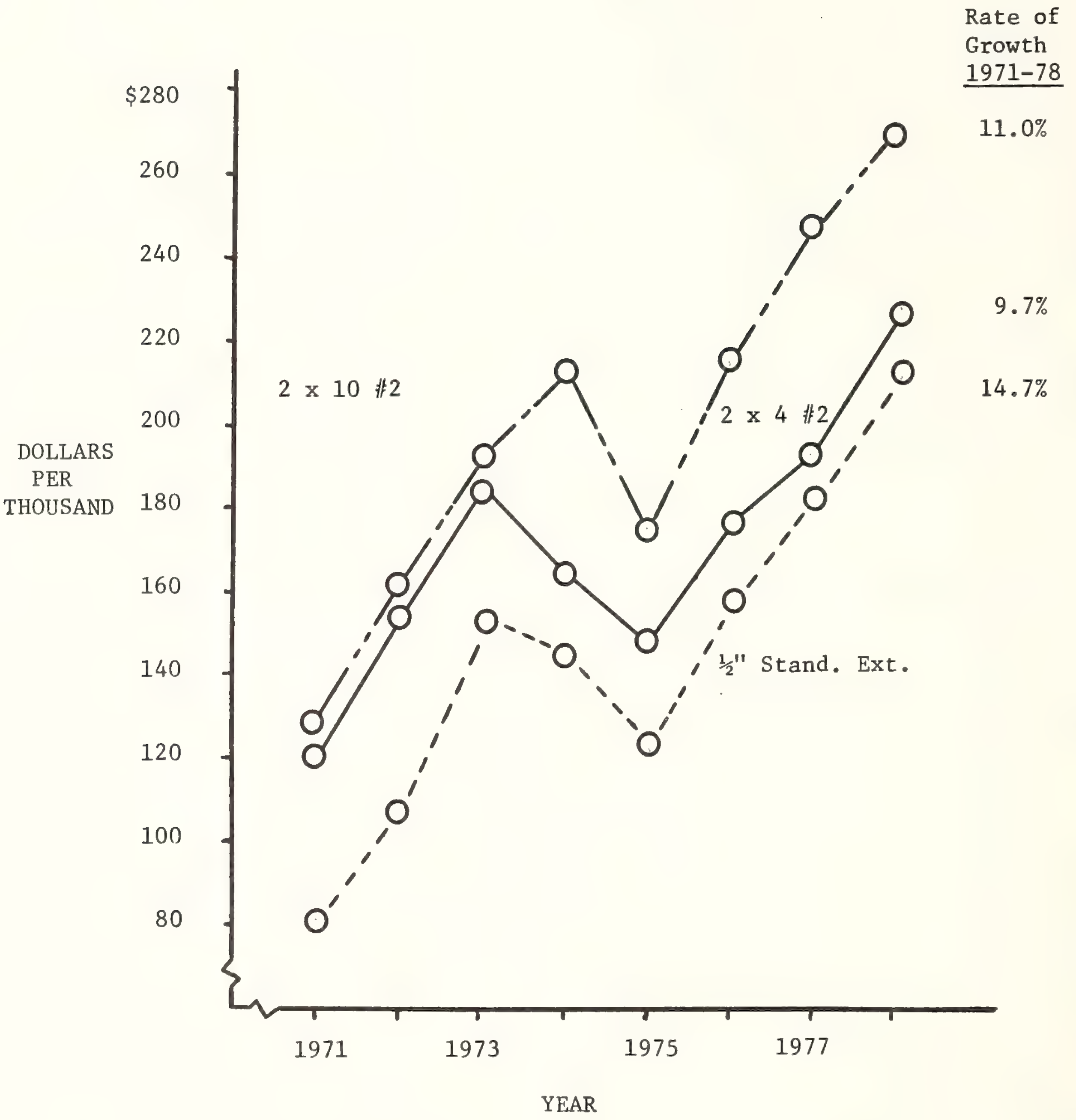
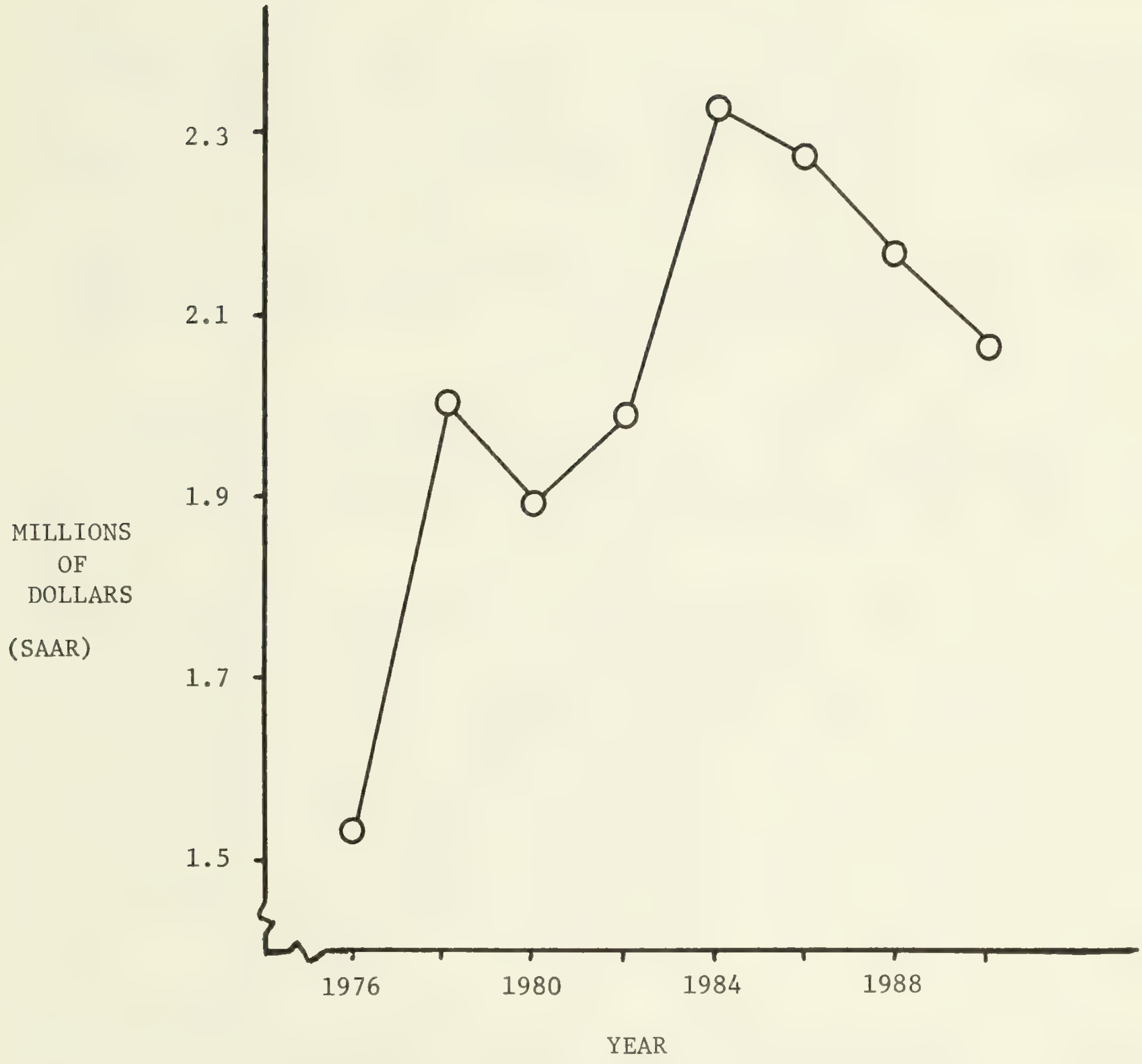


Figure 2. Total Housing Starts - U.S.



orchard? Could seed be collected by clone and only seed from the best general combiners used?

FUTURE

The rapid real price rise for southern pine stumpage mentioned previously is indicative of an impending softwood supply "crunch" across the South. A supply "crunch" which is not limited to specific companies or locations. The real problem however is that this tightening of supply corresponds to an unprecedented increase in demand for wood products. Figure 2 shows the projected number of housing starts through 1990.

The 1976 to 1984 increase (Figure 2) is the driving force behind current activity in the forst products industry. The 1978 level of starts, just over 2.0 million, had the industry running at capacity. The post-World War II babies will be at prime house-buying ages in the next few years. Demand for pulp and paper also cycles, but this industry is largely "mature" and growth is slower (2.5 to 4.0 percent) and less cyclic than for building products.

Also important is the fact that housing starts are projected to decline after 1985. This will heighten pressures for obtaining genetic gains faster. Right or wrong, young plantations are going to look increasingly attractive in the future, especially improved plantations.

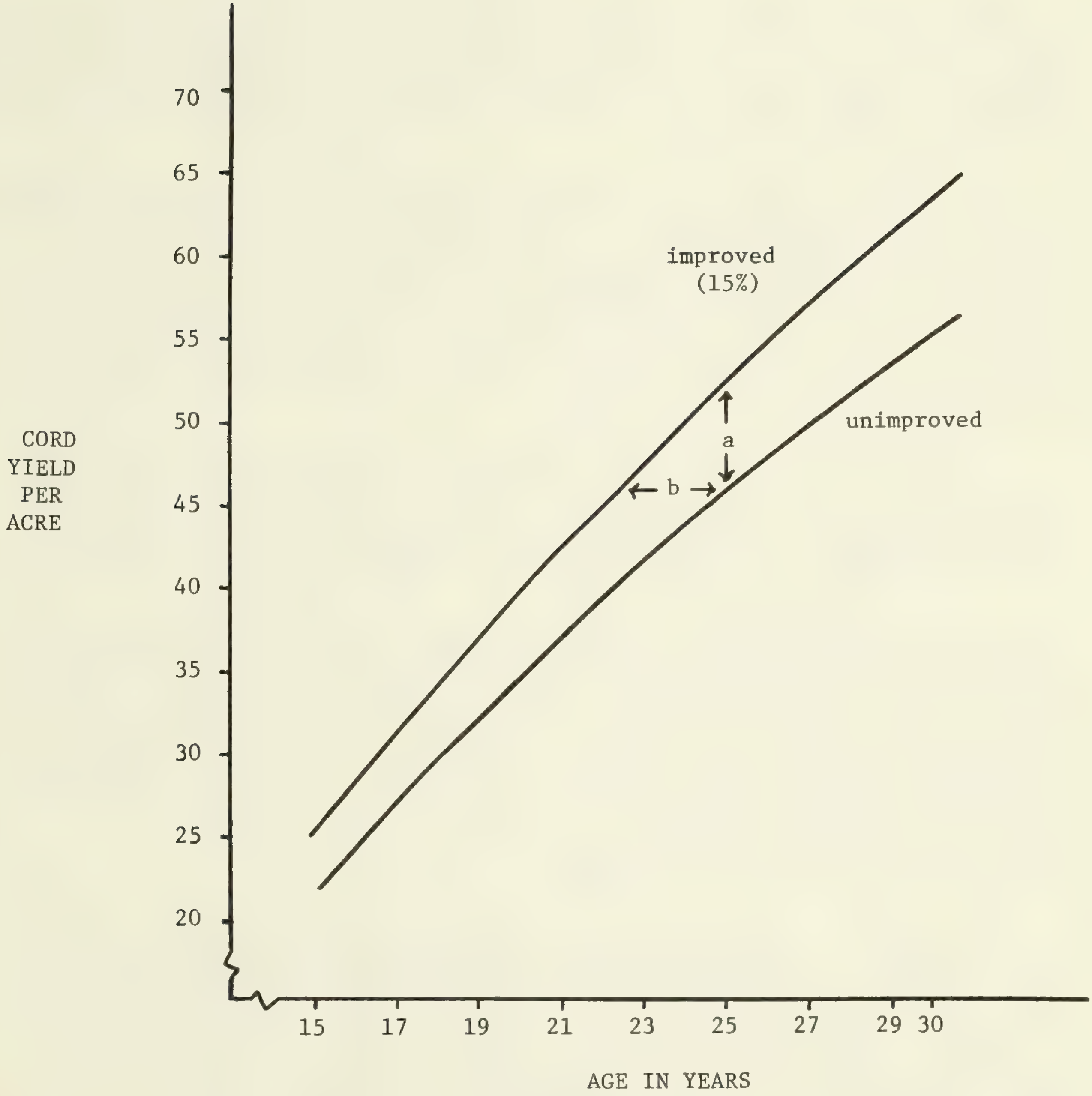
To illustrate, consider the two plantations portrayed in Figure 3. The unimproved yield is for plantations in Virginia and the data are relatively old (Dierauf and Marler, 1965). These yield data were used simply because they provided a yield estimate each year over the rotation. Other yield data would just as well demonstrate the point.

At age 25, the unimproved plantation is estimated to produce 45.8 cords or \$458 at \$10 per cord. The improved plantation, with a 15 percent volume gain, would yield 52.7 cords or \$527 at age 25. Using 10 percent interest, the present value of the difference represented by "a" in Figure 3 is \$6.37. On the other hand, a volume similar to the age 25 yield of the unimproved stand is attained by the improved stand in 22 years. The improved stand yields 45.2 cords in 22 years. The present value of 45.2 cords at 22 years is \$13.24 higher than that for 45.8 cords at 25 years (difference "b" in Figure 3). In other words, it is worth twice as much to harvest the improved stand earlier than to wait for the improvement at the old rotation age. Given this fact, and the demand projected in Figure 2, improved stands will probably be harvested sooner. This point has been stressed by Lambeth (1978) also.

Genetic gains above 15 percent, that is to the left of the improved yield in Figure 3, simply mean that stands may be cut even earlier. Actual financial maturity on the stump occurs earlier than age 25, but harvesting costs, as a function of stem size, dictate a later harvest. However, harvesting efficiency would be very similar with yields at age 25, unimproved, and age 22, improved.

Of concern is the matter of juvenile vs. mature wood if improved stands are to be harvested earlier. Bendtsen (1979) concludes that, relative to mature wood, juvenile wood has shorter fibers, larger fibril angle, lower

Figure 3. Yield of Virginia Plantations With and Without Genetic Gain



specific gravity and percent of latewood, has irratic and typically greater longitudinal shrinkage, greater amounts of spiral grain and compression wood, and is lower in strength. These factors have a particularly adverse effect on the use of greater amounts of juvenile wood for solid wood products. Pearson and Gilmore (1979) also conclude that young, fast growing trees are of lower density and strength and Bendtsen (1979) suggests that design codes may have to be altered for material from fast growing plantations. Breeding trees with high density juvenile wood or that have a more rapid transition from juvenile to mature wood should be increased in priority.

Another means of meeting rising future demand for timber products is for an organization to acquire more forest land. Purchase of forest land increases the proportion of controlled timber during periods of peak demand. But, in the next 5 to 10 years, there will be substantial acreage of improved plantations available and these plantations will be of great benefit since they will reduce additional land needs.

For example, consider the simplified case of a firm that currently harvests 300,000 cords of wood annually from its land to meet minimum backup standards. With an average unimproved yield of 2 cords/acre/year over a 25 year rotation and under ideal regulation conditions the firm would require a land base of 150,000 acres. Now suppose that in the mid to late 1980's, mill size increases by 50 percent in the face of increased demand. The firm now needs an annual harvest of 450,000 cords and consequently a larger controlled land base. In fact, using 50 cords per acre at age 25, the firm needs 75,000 additional acres to maintain a fixed fee timber backup.

If, however, the firm is in a position to take advantage of higher yields from improved stands in the future, its additional land requirements are greatly reduced. A 15 percent volume gain at age 25 (same rotation age assumed for simplicity) from improved plantations would increase yield to 57.5 cords. Only 45,652 additional acres are needed with improved plantations.

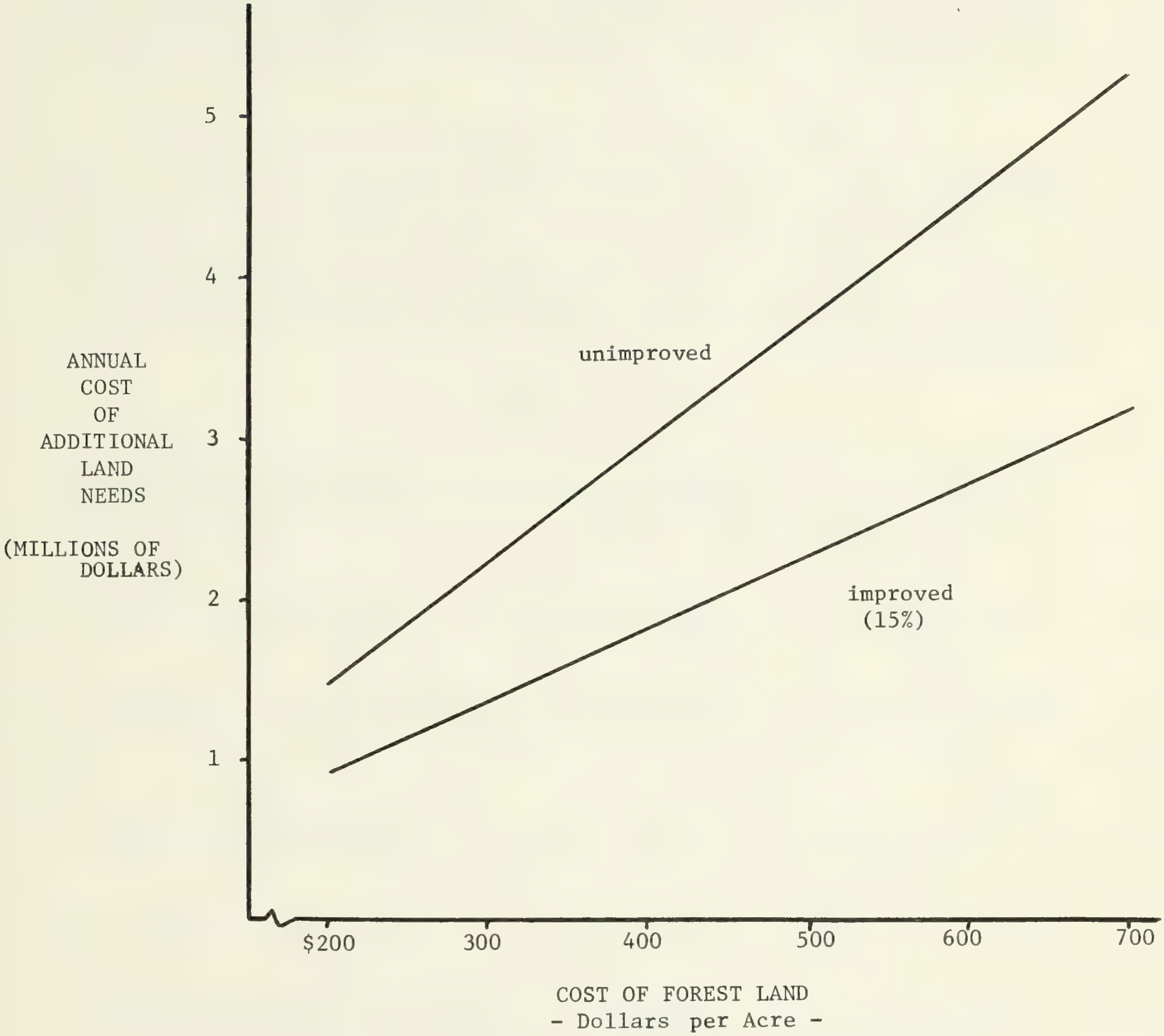
The difference in annual interest charges for the purchase of additional forest land, if unimproved vs. improved plantations are available, is depicted in Figure 4. As the cost of forest land (including standing timber) increases, the magnitude of the difference also increases. At $500 per acre, there is a savings of $1,500,000 per year directly attributable to tree improvement. Furthermore, to this savings in annual interest (or opportunity) charges must be added the savings in property taxes and management costs associated with the smaller land base requirements with improved plantations.

SUMMARY

This anlaysis of the economic value of tree improvement activities has been purposely broad. It has considered the market environment within which tree improvement work is important. This overall perspective, especially given the future wood products demand situation, shows that past economic evaluations of tree improvement have probably been very conservative. Tree improvement programs may well move from good to excellent investment status. This fact should be good news for the tree improvement specialist.

However, recent trends and recognition of the leverage that tree improvement provides almost surely mean that tree improvement activities are

Figure 4. Annual Cost Associated with Additional Lands Needed After Mill Expansion.



considered an integral part of operations - certainly no longer research. As such, tree improvement work faces the same day-to-day operational pressures as other phases of the business. Consequently, there is going to be growing impatience with the current pace of genetic improvement and probably an increasing need to clearly define both breeding and operational goals for tree improvement.

I am afraid that we have stressed tree improvement costs too much in the past. That is natural in the early part of such a long-term venture as tree improvement, but the emphasis needs to change. In the future, questions of cost are going to be secondary to questions of added return (yield) and the timing of such returns.

The past emphasis on costs has also made us somewhat conservative as to approach. Particularly given future demand levels, forest industry will be willing and indeed actually called upon to take substantial risks. I challenge the tree improvement specialist to do the same; take some risks. More research is needed relative to genetic gain sooner and/or increasing its magnitude. If this means a narrowing of the genetic base, so be it. Simply make an effort to keep such practices outside the long-term breeding scheme. The tree improvement specialist has never been in a better position to contribute to southern forestry.

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INDEX SELECTION FOR VOLUME AND STRAIGHTNESS IN A LOBLOLLY PINE POPULATION

Floyd E. Bridgwater and Roy W. Stonecypher[1]

Abstract.--Relative economic values for stem volume and bole straightness score were experimentally determined for use in combined family, and multiple-trait selection indexes. Selection indexes were constructed for a population of loblolly pine using different sets of relative economic values and sensitivity of genetic gain in total economic value to these changes was determined. Predicted gains in total economic value were relatively insensitive over a substantial range of relative weights.

Keywords: Selection index, relative economic values, sensitivity analysis, *Pinus taeda*.

Tree breeders must select on the basis of several traits to maximize genetic gains and returns from tree improvement. Faster growth is usually the primary criterion for selection, but other traits like wood density and bole straightness may strongly influence yields of specific products and the economic value of trees.

The improvement of several traits can be accomplished by tandem selection to improve one trait at a time, or by selecting only individuals that exceed culling levels for each trait. However, index selection has been shown to be theoretically superior to either of these (Hazel and Lush, 1942). Also, the accuracy of selection may be increased when information from relatives is considered in addition to information from candidate trees. The theoretical advantage of such indexes for seed orchard rogueing was demonstrated by Namkoong (1965). Information from relatives and for multiple traits can be incorporated in a combined family and multiple trait index and these have been used in applied forest tree selection programs (Arbez et al., 1974, Wilcox et al., 1975). Even though the theoretical advantage of combined multiple-trait indexes is clear, several problems have limited their use by forest tree breeders (Namkoong, 1969, Arbez et al., 1974). Selection indexes combine economic and genetic information in a multiple regression equation to predict the worth of an aggregrate genotype. Non-linearity or discontinuities in value functions make indexes more difficult to construct, or even inaccurate, and future trait values are uncertain. Unavailable or inaccurate estimates of economic or genetic values also have limited the use of selection indexes in forest tree improvement. An index based on poor parameter estimates is unlikely to be optimum (Williams, 1962).

The lack of reliable estimates of relative economic values may be the factor most limiting the use of selection indexes in forest tree breeding. The manner in which changes in specific traits impact total value has been described only for a few traits influencing pulp or paper yields or quality, (van Buijtenen, 1974). Studies estimating relative economic values for traits affecting yields or quality of solid-wood products are few.

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This paper describes a procedure to estimate relative economic values for volume and straightness for planted loblolly pine, (*Pinus taeda* L.). These values were used to construct selection indexes and to determine the sensitivity of selection results to changes in relative economic values.

METHODS

Approach

Detailed stem measurements were taken from 11-, 12-, 13-, and 14-year-old trees felled in progeny tests. A yield model and a merchandising simulator were used to forecast volumes and the value of products that could be realized from each stem at age 25. Linear regression was used to determine how changes in volume and in subjectively determined straightness scores were related to forecasted values for individual trees. These relative economic values were used to construct selection indexes and to determine the sensitivity of the index to changes in these values.

Straightness and Value Determination

Trees selected for this study were from Weyerhaeuser Company's supplemental genetic tests near Piney Green, North Carolina. Trees were selected using data recorded in the spring of 1978. Ninety trees were chosen from the eight plantations (North and South Coastal tests planted in 1964, 65, 66 and 67). Twelve trees were selected in each of six straightness classes (1 thru 6), to represent the range of diameters and heights in the tests. Straightness scores were subjectively assigned to each tree based on degree of sweep, spirality, crooks, and lean relative to other trees in the test planting (Anonymous, North Carolina State University). A score of 1 was assigned to the straightest trees.

Diameter outside bark, bark thickness, and stem deviation from a string line from the center of the butt to the center of a 2" top were measured for each 2' 1" segment on felled trees.

Measurement trees averaged 12.5 years of age from planting. Basal area, trees per acre, minimum and maximum diameter, and average height of the dominant and co-dominant stand were inputs to a yield model which estimated the current yield from stand tables and then projected the stand table to forecast yields at age 25. The assumption was made that each tree maintained its relative position in the stand table from age 12.5 to age 25 (Strub, 1979). Height at age 25 was estimated by adding the difference between current and 25-year height to measured height at age 12.5 Actual and projected stand parameters are shown in Table 1.

Table 1.--Parameters for actual and projected stand

	Actual stand at age 12.5	Stand at age 25
Mean D.b.h.	5.9 in. (15.0 cm)	8.5 in. (21.6 cm)
Std. Deviation	1.1	1.3
Mean Height	39.1 ft. (11.9 m)	68.4 ft. (20.8 m)
Std. Deviation	4.1	4.8
Mean Volume	---	10.4 ft.^{3} (0.29 m^3)
Std. Deviation	---	3.9

A taper model used measured and forecasted diameters and heights to estimate diameters for each 2' 1" segment at age 25. Estimates from the taper model were input to a merchandiser simulator to estimate the worth of each tree. Value of each stem was the value of products less mill processing costs. These may vary significantly from processor to processor, and over time. The total log volume was classified into chip-n-saw, chips, or plywood for each straightness class (Table 2). The forecast growth above the measured height was assumed to be straight for every tree. This portion of the bole was too small to contribute significantly to chip-n-saw volume and therefore had little impact on differences among trees in total value. That is, our model chipped the upper portion of the stem assumed to be straight.

Table 2.--Summary of log values from a merchandising model

	Value $ Per Tree			% of Log Yield		
Strt. Class	Avg.	Min.	Max.	Chip-n-saw	Chips	Plywood
1	10.18	1.12	22.21	70.42	29.58	----
2	10.85	1.10	23.11	70.75	29.25	----
3	9.41	1.16	23.52	64.56	32.16	3.28
4	9.39	1.21	26.18	68.62	31.38	----
5	8.13	.99	19.80	58.14	35.44	6.42
6	7.89	.96	22.39	56.26	43.74	----

Estimating Relative Economic Values

A Kruskal-Wallis one-way analysis of variance showed no significant differences among mean tree total values for 6 straightness classes at the .80 confidence level. Moreover, the range among mean values for the 6 classes was small ($2.29) when compared to the mean range of values within straightness classes ($21.78). This suggested that most of the variation in value was related to size.

Covariance analysis was used to compare linear regression of value on volume for the 6 straightness classes. The regression model was $\hat{Y} = b_0 + b_1 X$ where; Y is the total value per tree and X is volume per tree. The apparent similarity between classes 1 and 2, 3 and 4, and 5 and 6 led us to compare three combined classes; i.e., 1 + 2, 3 + 4, and 5 + 6 (Table 3). Slopes of these three lines were not statistically different at the 90% confidence level. Regressions differed in level between classes 1 + 2 versus 3 + 4 and 3 + 4 versus 5 + 6 at the 99% confidence level.

Economic values for volume and straightness score were determined by calculating the change in average tree value per unit change in each trait.

Table 3.--Regression equations for three combined straightness classes

Straightness Class	b_0	b_1	Volume/Tree (cu.ft.)	Average Value Per Tree at Mean Volume $\hat{\bar{Y}}$ ($)
1 + 2	-6.59	1.82	10.6	12.34
3 + 4	-6.15	1.68	10.5	11.32
5 + 6	-6.06	1.55	10.2	10.06
All Classes Combined		1.68	10.4	

The change in stem value associated with a unit change in volume was estimated by the slope of the regression through all points in all three classes combined; i.e., $1.68. Average value per tree was adjusted for differences in average volumes among straightness classes by calculating $\hat{\bar{Y}}$ at the overall mean volume (10.4 cu.ft.) for each class (Table 3). Adjusted value per tree increased from $10.06 for class 5 + 6 to $12.34 for class 1 + 2. Therefore, the average increase in value for each unit of straightness score was ($12.34 - $10.06)/(5.5 - 1.5) = $2.28/4 = $0.57. The relative economic values for volume and straightness were then; $1.68/$0.57 ≅ 3:1.

Index Selection

Combined family, multiple-trait indexes were constructed following procedures described by Wilcox, et al. (1975). These incorporated individual and full-sib family information for each trait in a single index value assigned to every tree in a test. We assumed that the components of variance (or covariance) for full-sib family means estimated half the additive genetic variance (or covariance) in constructing indexes for each test.

Narrow-sense heritabilities for volume and straightness on an individual basis are presented in Table 4 as well as genotypic correlations between the two traits. Standard deviations were calculated from estimates for the eight tests. Selection to improve straightness would be easier than for increased volume since it has a higher heritability. The average genotypic correlation between volume and straightness (-.152) indicates a positive relationship since decreasing straightness scores indicate improved straightness. This positive genotypic correlation indicates that selection for volume or straightness will result in improvement in the other as well.

Selection indexes were constructed for four sets of relative economic values: (1, 0), selection for volume improvement-straightness score not considered; (1, -0.33), straightness given one-third as much weight as volume; i.e., our experimentally-determined set of weights; (1, -0.5), straightness given one-half as much weight as volume; and (1, -1), both traits given equal weight.

Table 4.--Narrow-sense heritabilities and genotypic correlations for eight genetic tests used to construct selection indexes

Test	Heritability		Genotypic Correlation
	Volume	St. Score	
North Coastal - 1964	.30	.55	-.210
65	.29	.40	-.384
66	.35	.29	-.134
67	.17	.24	-.072
South Coastal - 1964	_1	.35	_1
65	.23	.27	.179
66	.17	.26	-.376
67	.15	.25	-.070
Mean	.24	.33	-.152
Std. Deviation	.08	.10	.215

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[1] Estimate of family variance component for volume was negative, and these values were not included in further analysis.

All indexes were calculated using the same genotypic and phenotypic parameters. Therefore differences in expected genetic gains were the result of changing economic emphasis on volume and straightness score. Expected genetic gains in each trait from "pick-the-winner" selection based on index scores are given for each set of weights in Table 5. The proportion saved was 2% from each test. Percentage expected genetic gains were calculated by dividing the mean genetic gain for each trait by its respective average over all tests. These were 11, 12, 13, and 14 years of age.

Table 5.--Average expected genetic gains from selecting in eight genetic tests

Relative Economic Weights[1]	Expected Genetic Gain Average Age 12.5[2]	% Gain	Straightness Score	
(1, 0)	0.99 (cu.ft.)	37	-0.32	10%
(1, -0.33)	0.94	35	-0.64	19%
(1, -0.5)	0.89	32	-0.75	23%
(1, -1)	0.73	28	-0.94	29%

[1] (Volume weight, straightness weight)

[2] Average age for 11-, 12-, 13-, and 14-year-old tests

Traits other than volume and straightness were not considered in the selection procedure; e.g., trees infected with fusiform rust, (Cronartium fusiforme Hedge and Hunt), or which had poor crown scores were not excluded, nor was relatedness among selects restricted. This was done to simplify the sensitivity analysis.

Sensitivity Analysis

We examined the expected change in total value for sensitivity to changing relative economic weights in selection indexes. This was determined by multiplying the predicted gain in volume and straightness (Table 5) by their respective economic values ($1.68/cu.ft. volume and $0.57/unit straightness score). This assumed that economic values for the two traits were the same at mid-rotation age and 25 years. These products and their sum, which is the expected net total value, are presented in Table 6 for each selection index. Sensitivity to changing index weights was calculated as a % of the net total gain predicted for our experimentally-determined set of economic weights.

Results and Discussion

Assigning no economic weight to straightness resulted in greater predicted genetic gain in volume than for any other set of weights, as expected. Predicted gains increased for straightness score and decreased for stem volume as proportionately greater weight was assigned to straightness score (Table 5).

Predicted change in net total value was reduced from our optimum set (1, -0.33) by 5% for both (1, 0) and (1, -0.5), (Table 6).

Table 6.--Expected genetic gains from index selection based on different relative economic values

	Expected Genetic Gain in Economic Value ($)			
Relative Economic Weights	Stem Volume	Straightness Score	Net Total Value	% of (1, -0.33)
(1, 0)	1.66	0.18	1.84	95
(1, -0.33)	1.58	0.36	1.94	100
(1, -0.5)	1.50	0.43	1.93	95
(1, -1)	1.23	0.53	1.77	91

The contribution of stem volume to expected genetic gain in total economic value (1.66) was greater for (1, 0) than for the optimum set (1.58), however, this was offset by a greater contribution for straightness score (0.36 vs. 0.18) for the optimum index. Values for stem volume were lower than for the optimum index when straightness score was given more relative weight. Associated increases in value for straightness score were not large enough to offset these decreases and thus net total economic value was highest for the optimum index.

Predicted change in net total value was relatively insensitive to changes in relative economic weights in the range we examined. The 9% decrease in gain in net total value from the optimum index when the two traits were given equal weight (Table 6) represents approximately a 3% decrease in the net total value of the average tree at age 12.5. When unknown, but significant, weight is assigned to straightness score in the selection process, gains in net value for our model could be well below those for the range of relative weights considered. We reemphasize that these results apply only to our model. Specifically, one in which merchandising for the highest value product yields mostly chip-n-saw logs. Also, significant changes in manufacturing costs or market prices will necessitate a reexamination of these conclusions. Changes in genetic parameters for the selection could also affect the outcome of an analysis like the one presented. For example, if stem volume and straightness score had a negative genetic correlation, selection for increases in one would imply decrease in the other, and perhaps greater sensitivity over a relatively small range of economic weights.

We recommend that when economic values are not easily determined, sensitivity analysis be done on the selection population to determine the impact of varying relative economic values. If one can confidently conclude that the true relative values for traits of interest lie in a range of values to which predicted genetic gains are insensitive, the costly process of determining economic values can be avoided.

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INCORPORATING GENETIC INFORMATION IN GROWTH AND YIELD MODELS

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Abstract.--In tree improvement programs, biological differences resulting from selection and breeding should be quantified in such a way that they can be incorporated into yield prediction systems. Only if this information is included in growth and yield models can genetic gain be estimated by comparing improved-tree yields with woods run material for specific management regimes. In this study, we selected an individual tree model for loblolly pine and modified four relationships that reflect genetic differences, then we compared yields with woods run material. Gains and losses for the various systems are reported.

Additional keywords: Genetic gain, loblolly pine, simulation

INTRODUCTION

The goal in tree improvement is to increase productivity by using genetically improved planting stock. Quantitative estimates of increased productivity are needed if forest managers are to make reliable management decisions on the production and use of improved stock.

Ideally, estimates of increased production should be based on the difference in yield of improved stock over nonimproved stock for a specific management regime (such as stocking levels, rotation age, intensive cultural methods, thinning practices and prospective utilization). This approach recognizes that the genetic gain of a given clone, family, or mixture is not stable or fixed but may vary among management regimes.

We propose that tree improvement programs should concentrate on defining biological differences produced through selection and breeding and that these differences should be quantified in such a way that they can be incorporated into yield prediction systems. In this way genetic gain can be estimated in yield prediction systems for specific management regimes. With these genetic gain estimates, managers could assess the potential value of improved stock to their operation and determine how to modify management practices to maximize gains from available improved stock.

Reasonably accurate yield prediction systems (or growth and yield models) for southern pines already exist for natural stands, plantations on old field sites, and plantations on cutover and site-prepared land (Burkhart 1979).

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Current research in this area is oriented toward extending existing models or constructing new models for intensively managed plantations--incorporating cultural methods such as thinning, fertilizing, using genetically improved stock, irrigating, bedding, and controlling vegetation. One model (Daniels and Burkhart 1975) for loblolly pine plantations incorporates some fertilizing, thinning, and site preparation alternatives but does not include using improved stock.

We selected Daniels's and Burkhart's model for loblolly pine and studied ways in which it might be modified to incorporate genetically improved stock as a cultural treatment. We have neither developed a new model nor incorporated all possible improved stock options in this one, but we hope that our ideas will stimulate interest in growth and yield modeling among tree improvement researchers. We in tree improvement have data resources for improved stock that ought to be used; and unless we become active, future growth and yield models may not incorporate our ideas or data.

The model developed by Daniels and Burkhart is implemented for digital computers in the FORTRAN language and consists of a main program (PTAEDA) and several subroutines (INPUT, PLANT, JUV, COMP, THIN, PREP, FERT, and OUTPUT). The model is basically a stochastic simulator which accepts initializing parameters such as initial spacing, site index, and cultural regimes from the user (INPUT); assigns coordinates to individual "trees" in computer memory (PLANT); "grows" the juvenile or pre-competitive "stand" according to a diameter distribution model and several growth relationships (JUV); and determines the "growth" and "survival" of each tree under a competition model based on distance and size of nearest neighbors (COMP). Cultural treatments such as fertilizing (FERT), thinning (THIN), and site preparation (PREP) may be imposed on the developing stand.

The juvenile or pre-competitive stand is "grown" in this way. First, the age (since establishment) at which crown closure will occur is predicted. This age marks the beginning of competition, and its prediction depends upon the expected number of surviving trees (TS) at each age (A) after planting with a given number of trees per acre (TP) on a site with a given site index (SI) based on 25 years. Once this age is determined, the height of dominant-codominant trees in the stand (HD) is predicted. Next, the minimum (DMIN) and average (DAVE) diameter at breast height for the stand is predicted, and a diameter distribution is generated in the form of a Weibull. Surviving trees are selected at random and assigned diameters by sampling from this distribution. Finally, each surviving tree is assigned a total height (H) by a prediction equation using DBH, HD, TS, and A as well as a crown length (CL) using total height minus clear bole length (CBL), which is predicted using H, DBH, TS, and A.

Two features of the juvenile stand likely to be modified by genetics are the height over age (site index) curve and the phenotypic variance of growth traits. We know that by selection and breeding, early height growth can be increased and genetic variance reduced. Although the height growth curve for this model is monomorphic, we modified it to accept early and/or later height growth changes--in effect, polymorphic forms. Height growth increases lasting through age 25 are equivalent to increasing the site index. We also modified the model to allow for reduced phenotypic variance in all juvenile growth traits. This is considered equivalent to restricting genetic variation as, for example, in single family plantations. Once the modified juvenile stand is established, we allowed the model to "grow" the stand through competition (COMP) without further modifications.

MODEL MODIFICATIONS

To determine the consequences of genetic modification of this model, we posed four situations representative of what might happen in a tree improvement program. For site index (SI) 50 and SI 75, we compared the results of the four situations with a nonimproved stand, designated WOODSRUN. For all situations, our "stands" started with 8 x 8 foot spacing on old-field sites with no thinning or fertilizer. These four situations are shown below as A - D.

(A) We increased height growth 6 feet above that predicted for WOODSRUN at time of crown closure, then gradually reduced this 6-foot gain to zero by age 25. We assume that site productivity is fixed, or that height at age 25 (site index) cannot be increased through genetics. We refer to this situation as JHD6.

(B) We posed the same situation as (A) but maintained the early 6-foot height gain to age 25. We assume that genetics can influence site index as measured at age 25. We refer to this as MHD6 and show SI to increase 6 feet.

(C) In tree improvement programs, a shortage of improved seed is likely to occur at some time. One way to maintain planted acreage is to mix improved seed with regular seed. We constructed a mixed juvenile stand by randomly mixing half WOODSRUN and half improved trees (MHD6) and let the model "grow" the mixture. We refer to this as MIX.

(D) Genetic variability of trees can be reduced, for example, in single family or single clone plantations. Since in this model we cannot separate phenotypic variance into genetic and environmental components, we simply reduced the total phenotypic variance by 1/2, 1/4, and 1/8 of the WOODSRUN--a situation that would result from using genetic material more uniform than WOODSRUN. We achieved this effect by transforming the diameter distribution at crown closure to a new diameter distribution with reduced variance and the same mean. Since all growth traits in this model are predicted from d.b.h., variance in all other growth traits were reduced similarly. We refer to these modifications as VAR 1/2, VAR 1/4, and VAR 1/8.

For the WOODSRUN and four modifications, we considered survival, average d.b.h., average height, standing cubic foot volume, mortality volume, trees dead since crown closure, and diameter distribution at ages 10, 15, 20, and 25. The comparisons are realistic only to the extent that the model mimics actual conditions. Also, our results serve only as an example of what can be studied and are not to be considered conclusive. A more thorough study than ours would include more variables and many more simulation runs.

RESULTS

When limited to WOODSRUN situations and comparing SI 50 with SI 75, the model predicts differences well recognized in silviculture (Fig. 1). On more productive sites trees generally are larger and the range of diameters is greater. Early survival is higher on better sites, but later mortality is greater because of more severe inter-tree competition. With situations (A - D) imposed, these principles hold.

(A) Increasing only early height growth results in a slightly higher final combined volume (standing and mortality) over WOODSRUN on SI 50 but no difference on SI 75. Average diameters and distribution of trees by diameter class basically were unchanged from those of WOODSRUN. This result suggests that in tree improvement programs where early height growth is not maintained for the rotation, volume gain by age 25 may be minimal.

(B) By adding 6 feet in the pre-competition stage and maintaining it until age 25, final yield of standing plus mortality volume was substantially increased on both SI 50 and SI 75. On SI 50 the major change was in standing volume while on SI 75 the major change was in mortality volume, apparently reflecting the principle that on better sites inter-tree competition begins earlier and kills trees sooner than on poorer sites. The mortality volume might be regarded as the volume harvested under the ideal thinning system--an operation where only trees expected to die were removed. This result suggests that in situations where early height growth gains are maintained, the increase in production can be substantial, although thinning may be required on better sites.

(C) For our MIX, total volume on SI 50 and SI 75 was higher than on WOODSRUN, but only slightly less than for improved seed as in (MHD6). For SI 50, the MIX standing and mortality volume was lower than for the 100 percent improved seed. However, the MIX exceeded average volume production of WOODSRUN and improved seed (MHD6). For SI 75, the MIX standing volume exceeded that of 100 percent improved seed (MHD6) but was less in total volume (standing plus mortality). On the basis of these results, mixing of seed would be more desirable than would separate plantings of woods run and improved seed.

(D) Reducing the phenotypic variance generally reduced total volume production over that of WOODSRUN, although it did so only slightly on SI 50. The same trend held for average diameters. Survival was better than for WOODSRUN for all levels of reduced variance. In biological terms, reduced variance produces stands in which trees grow more uniformly. Trees are crowded, but without strong expressions of dominance, and death is delayed. This result mimics that expected for poor sites--higher survival and reduced competition. The disadvantages of decreased volume by reducing variance might be offset by production of a more uniform product and other factors that determine product value. In terms of product options, reduced variation could be a disadvantage, especially if longer rotations were considered.

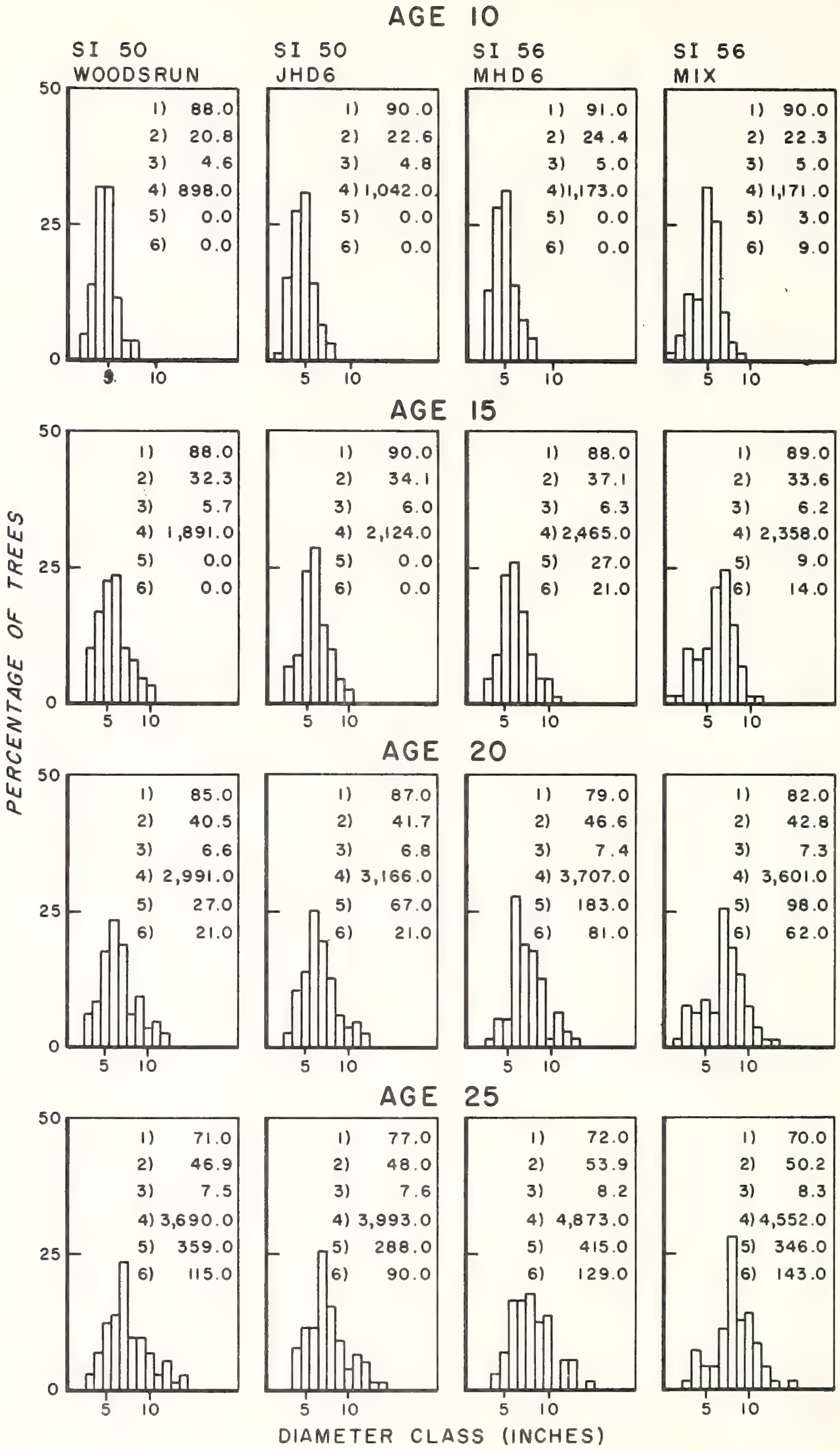
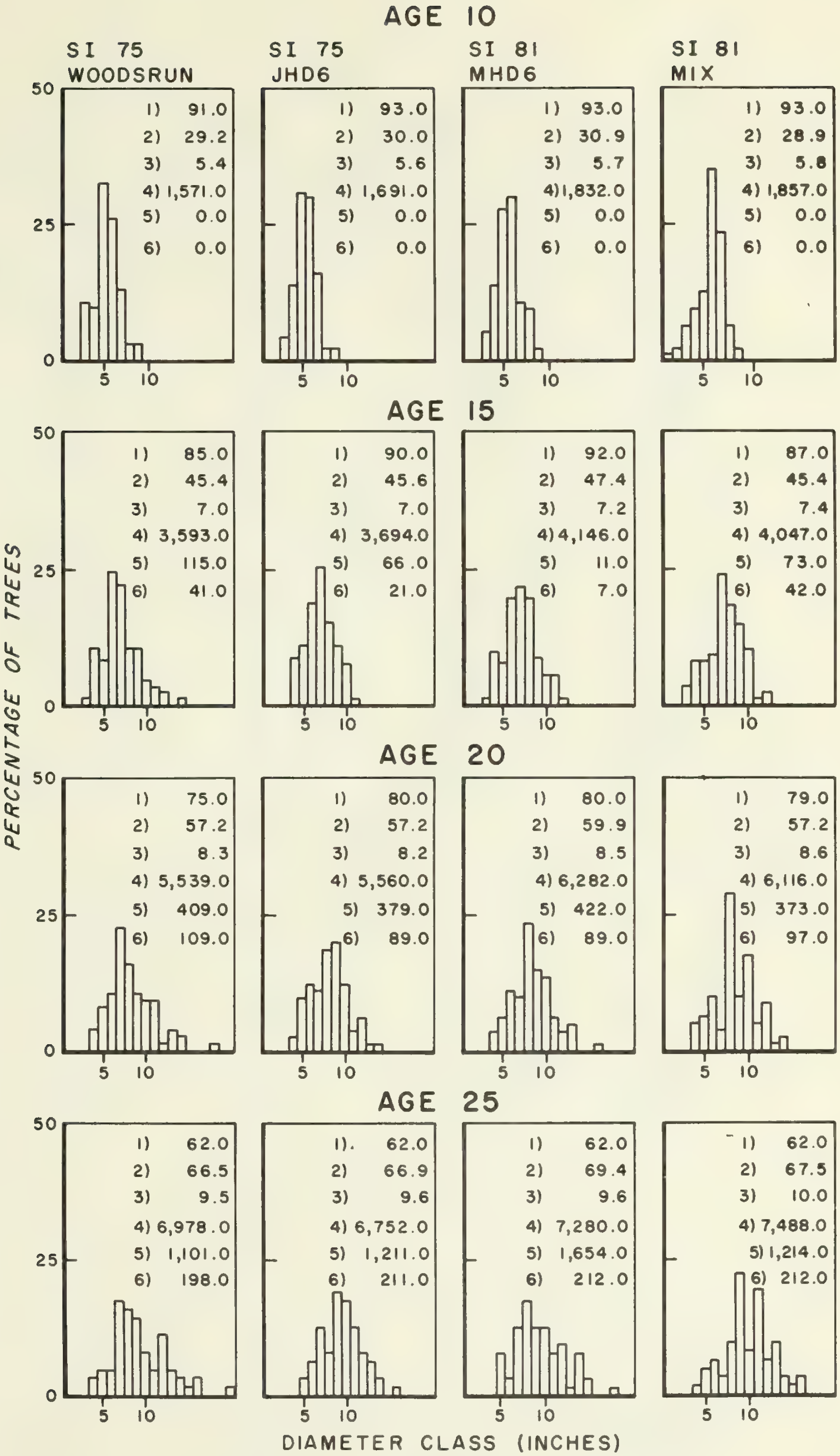


Figure 1.--Percent trees by diameter class, age, and situation. The values for each distribution include: (1) percent survival, (2) average height of dominants and co-dominants (feet), (3) average DBH (inches), (4) volume of standing trees (cu. ft.), (5) cumulative volume of trees dead (cu. ft.), and (6) number of trees dead since crown closure.



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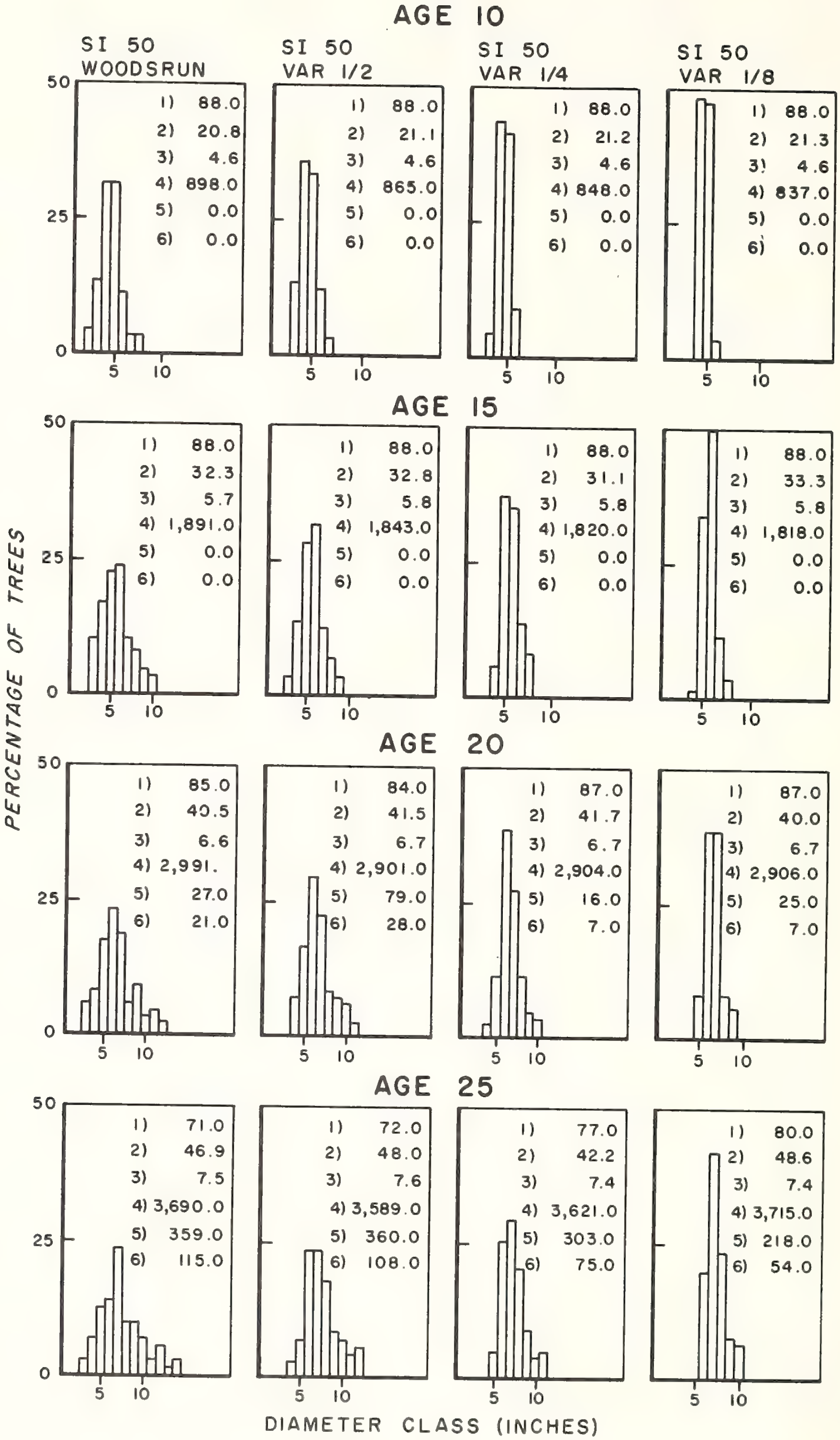

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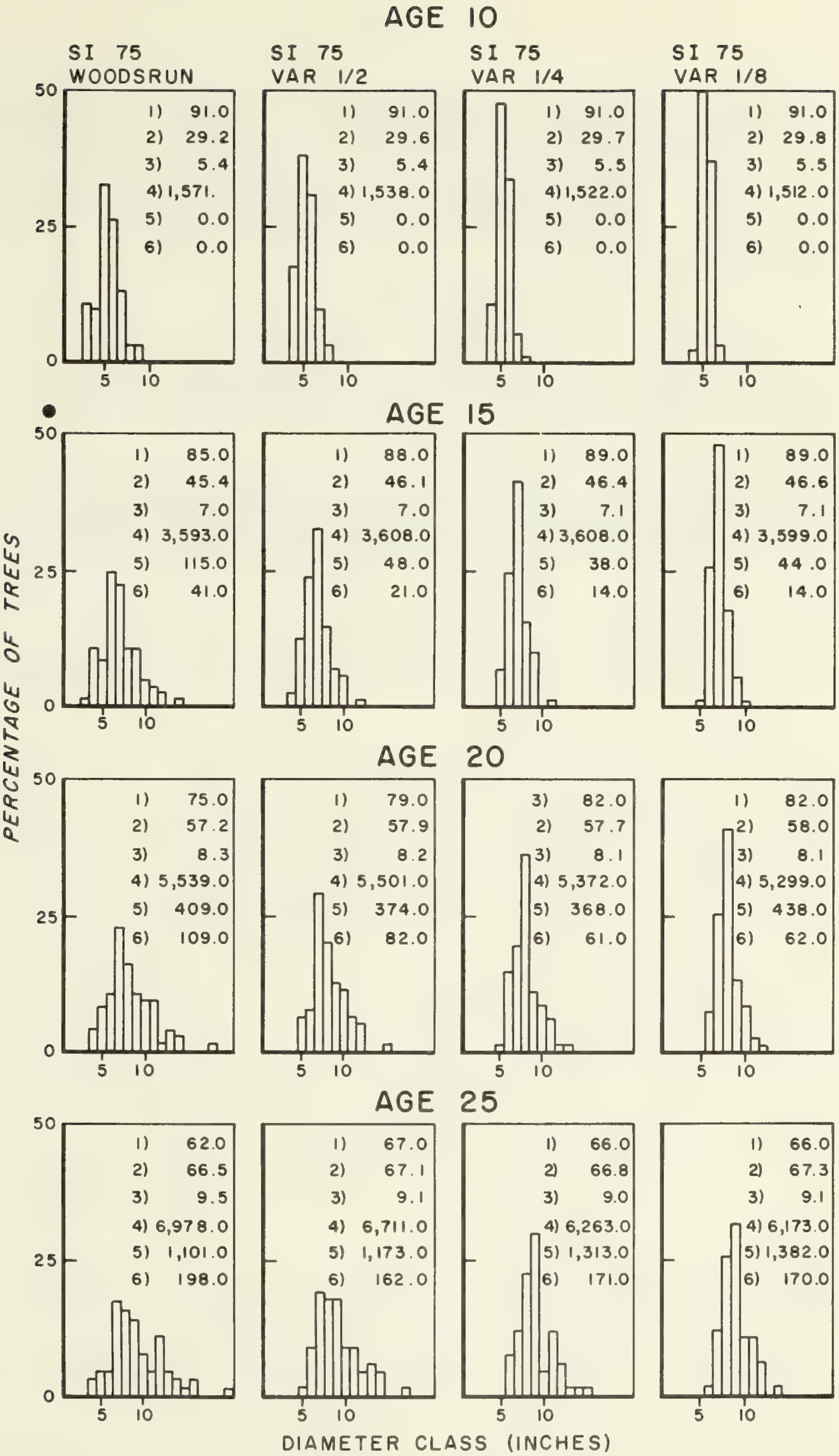

Figure 1.--Continued.

These four situations show genetic modifications in growth and yield prediction systems. Further modifications and genetic research in the growth and yield area should be pursued. Using data from improved stands, researchers need to study the growth relationships (equations) that are the basis of the model. Through these types of genetic studies, and in cooperation with growth and yield researchers, realistic estimates of improved stock productivity can be provided.

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The Use and Selection of Trees for Energy and Chemicals

Michael Williford, R.C. Kellison, D.J. Frederick,
and W.E. Gardner[1]

Abstract - High costs and unreliable availability of fossil fuels and petroleum-based chemicals have caused consideration of growing and using woody biomass as a source of energy and chemical feedstocks. Woody biomass is displacing or supplementing conventional fuels for many forest industries and some non-forest industries. Long range energy and chemical production will involve greater utilization of existing forests and short rotation plantations. Ideally, species used in these plantations should be selected for survival, growth and optimum energy and chemical yields. In practice, however, priority will be given to species and individuals that have already been selected for their growth, form, and wood properties. This paper considers the selection options and summarizes the current work being done through Department of Energy projects and commensurate work at N. C. State University.

Coping with the "energy crisis" has become a way of life in today's world. High fuel prices and shortages are readily apparent and the supply of petroleum-based chemical feedstocks is shrinking with accompanying higher prices for products derived from those feedstocks. An inexpensive, environmentally acceptable and renewable energy and chemical feedstock resource is needed to replace our traditional fossil fuel sources.

Wood is our greatest source of biomass and has potential to partially reduce our dependence on fossil fuels. Residues from many wood processing plants are being utilized as energy sources and numerous non-forest industries are converting to wood energy. Also, a considerable quantity of chemicals derived from wood--termed "silvichemicals"--are in use today (Bratt 1979). Numerous short and long term sources of woody biomass will be needed if a stable energy and chemical dependence is to be achieved. Already most forest residues are committed and low grade standing forests are being considered for short term biomass supplies.

Intensively cultured plantations using selected tree species are likely to become an important woody biomass source in this country (Fege *et al*. 1979). In South America, the largest energy plantation program in the world, over 200,000 acres (81,000 ha) per year is being established using various *Eucalyptus* spp. specifically selected for high energy yields. Trees are being grown on short seedling rotations with replanting done using genetically improved material rather than depending on coppice. Wood from these plantations is converted to charcoal for use in steel mill blast furnaces. Planting programs of this magnitude may occur in the United States if accelerated energy and chemical consumption continues.

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This paper discusses the current status and potential of genetic selection to increase energy and chemical production from trees used in plantation culture in the Southeast.

Species Selection

Establishing plantations to maximize production of woody biomass for energy or chemical feedstock production will require unconventional thinking. Characteristics such as wood color, working properties, or dimensional stability which in the past made certain species desirable are less or not at all important in energy or chemical production (Steinbeck 1978). Rather, the total above ground woody biomass produced per acre per year should be the primary species selection criterion. Other, less important tree characteristics related to end use include BTU yields, alpha cellulose content, and certain fiber characteristics. These attributes may be common to commercial species of timber value or to noncommercial species of indigenous and exotic origin. Both conifers and hardwoods have advantages and each will be used under certain conditions. Numerous species selection programs are underway to identify the best species for energy and chemical production (Bente 1979). Fast growing species such as green ash (*Fraxinus pennsylvanica* Marsh), red maple (*Acer rubrum* L.), water oak (*Quercus nigra* L.). willow oak (*Q. phellos* L.), sycamore (*Platanus occidentalis* L.), and loblolly pine (*Pinus taeda* L.) which have relatively high specific gravity and low moisture content are good candidate species (Kellison and Zobel 1971, Zobel *et al.* 1969). The physical characteristics and growth potential of the eucalypts and European black alder (*Alnus glutinosa* L. (Gaertn.)) make them particularly desirable for energy and chemical production in the South (Frederick *et al.* 1979). In general, species should exhibit rapid juvenile growth, adaptability to a variety of sites, low susceptibility to insects and disease and high genetic variability to maximize selection opportunities.

Site Selection

The next critical step to optimize production of woody biomass is matching species to site. As forestry is forced onto sites that are less than optimal, trade-offs must be made. Strains and species of trees must be identified and developed that are best suited for thse suboptimal sites--the swamps, ridges, and other areas unsuitable for agriculture. The Hardwood Research Cooperative[2/],

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[2/] The N. C. State Hardwood Research Cooperative consists of 19 forest industries and the N. C. Forest Service who own or control about 15 million acres (6 million ha) of land in the South from Delaware to Louisiana.

N. C. State University has been testing numerous commercial species for site adaptability for several years and evaluating their suitability for plantation management (Kellison *et al*. 1979). Results show loblolly pine superior in biomass production on most sites in the South with sycamore, sweetgum, willow oak, water oak, and green ash showing good potential for plantation management on many sites types. This type of testing must be continued and expanded to include the numerous noncommercial and exotic species as well. Our quickest and easiest gains in biomass yields will come from matching species to site.

Selection Within Species

Plantations of trees specifically grown for energy or chemical feedstock production will be established primarily on lands unsuited for agriculture or production forestry. However the increasing value of woody biomass for energy and chemicals may dictate expanded planting on the better sites. This fact is of particular concern because it may have far reaching effects on timber supplies and possibly food production.

Traditional tree selection programs have emphasized well-formed crowns, straight boles, and clean pruning for fiber and solid-wood products (Table 1).

Table 1. Superior phenotypes of southern hardwoods selected within the Hardwood Research Program.

Species	No. Graded	Species	No. Graded
Sycamore	149	Tupelo gum (*Nyssa aquatica* L.)	11
Sweetgum	129	Chestnut oak (Q. *prinus* L.)	8
Yellow poplar (*Liriodendron tuliplfera* L.)	65	Black oak (Q. *velutina* Lam.)	8
Green ash	75	White oak (Q. *alba* *L*.)	8
Red maple	27	Scarlet oak (Q. *coccinea* Muenchh.)	7
Willow oak	21	Swamp blackgum (*Nyssa sylvatica* Marsh.)	6
Water oak	20	Sugar maple (*Acer saccharum* Marsh.)	5
Northern red oak (*Quercus rubra* L.)	18	Southern red oak (Q. *falcata* Michx.)	5
Black cherry (*Prunus serotina* Ehrh.)	17	White ash (*Fraxinus americana* L.)	3
Black walnut (*Juglans nigra* L.)	12		
Cherrybark oak (Q. *falcata* var. *pagodaefolia* ELL.)	11		

Now these characteristics may be of minor importance in the production of woody biomass. In fact some researchers have expressed concern that traditional selection criteria have compromised or even had a negative effect on BTU and chemical yields from forest plantations (Kellison 1978).

Selection Criteria for Chemicals

Wood is a mixture of three natural polymers: cellulose 50%, hemicellulose, 25%, and lignin 25%. The exact percentage depends on species and genetic differences within species. Therefore, selection could be directed toward increasing that component which is most useful for producing chemical feedstocks. Cellulose content is most important in chemical yields because it makes up the largest component of wood and is the feedstock base for the most important chemicals. For example, cellulose can be converted to glucose and further fermented to ethanol which is an important industrial chemical and can be used for fuel. The conversion of glucose via ethanol to ethylene and butadiene represents the greatest potential utilization of cellulose for chemicals because of the importance of ethylene as the largest volume organic chemical and as a building block for petrochemicals and plastics, and of butadiene in the production of synthetic rubber (Goldstein 1978).

Likewise, a higher hemicellulose content which will yield primarily xylans from deciduous trees and glucomannans from conifers may be valuable. Lignin which will yield phenols may also be selected for but it is likely that selection for cellulose content will be most productive.

Invariably, the chemical industry must turn to a renewable chemical feedstock source and genetic selection programs will surely become important if tree plantations become the source of that resource.

Selection Criteria for Energy

Some of the characteristics desirable for chemical production are also desirable for energy yields, e.g., high cellulose or lignin content. However, BTU yield per unit volume appears to affect energy yields more than any other variable. Traits within and among species that affect BTU yields include specific gravity, moisture content, resin content, and extractive content among others.

Considerable variation in energy yields occurs between species but little is known about variation within species. Given the traits that influence BTU yield and knowing the variation of those traits within selected species (Table 2), it is assumed that breeding for gains in energy yields could be a profitable venture.

Fast growing trees traditionally selected for fiber and solid wood products will continue to be most desirable if the objective is total biomass production. However, this growth need not be concentrated in the bole as would be most desirable for solid wood products. Rather, a high biomass producing select tree may have numerous heavy branches and accompanying large widespreading crown and may even be multiple stemmed. Trees used for energy or chemicals will most

Table 2. Range in specific gravity and moisture content and average energy yields of selected Southeastern species.

Species	Specific Gravity	Moisture Content (Percent)	Energy yield(Dry) (BTU/lb)
Sycamore	0.41 - 0.49	76 - 138	8000
Sweetgum	0.41 - 0.53	98 - 145	7540
Green ash	0.48 - 0.66	41 - 68	8400
Red maple	0.40 - 0.58	55 - 100	8300
Water-willow oak	0.52 - 0.63	68 - 95	8000
Loblolly pine	0.42 - 0.68	70 - 160	8600

likely be whole-tree chipped so only total biomass production is important. Also, sprouting ability may become an important selection characteristic for hardwoods if repeated crops are to be grown on short rotations. However, if greater production gains can be achieved through breeding programs as compared to coppice rotations, coppicing may not be as important as many people have suggested. From Cooperative studies, we have found gains in volume production from use of genetically improved hardwood seed will exceed the commercial check by twenty-five percent (Zobel 1975). Similar gains have been reported for the Southern pines for which coppice management is obviously not an option.

A breeding program for developing species best suited for plantation culture might best be established by open-pollinated progeny tests of parent trees which had been identified by mild phenotypic selection. Members in the N.C. State Hardwood Research Cooperative have established seed orchards for a limited number of species which have plantation management potential in the Southeast (Table 3). Jett and Weir (1975) reported that the greatest volume gains of commercial hardwoods could be realized through a program of family and within-family selection followed by inclusion of the select trees in clonal seed orchards. An illustration of the potential gain to be realized from family and within-family selections is provided by Webb, et al. (1973) for a young sycamore plantation in Georgia. Of 64 families, tested, the two best produced 60% more dry matter than the plantation average while the two poorest produced 35% less than the average. Individual selection within these and other good families would result in even greater gain. A further finding was high genetic correlation between root collar diameter and dry weight per tree. This parameter could be used for initial selection while other traits are being evaluated in long term breeding programs.

At present, specially adapted sources of loblolly and sand pines (*Pinus clausa* (Chapm.)) Vasey have been developed for droughty sites in the South. Also, specially selected sources of loblolly and pond pine (*Pinus serotina* Michx.) have been found very adaptable to wet sites (Zobel 1979). Numerous other southeastern species have sufficient variability for selection of desirable energy and chemical characteristics or adaptability to specific sites.

Table 3. Hardwood seed orchards by species and acreage in the Hardwood Research Program.

Species	No. Orchards by Type		Acreage of Orchard by Type	
	Clonal	Seedling	Clonal	Seedling
Eucalyptus	1	2	1	2
Green ash	1	-	2	-
Sweetgum	6	1	37	4
Sycamore	8	2	18	6
Water-willow oak	5	1	15	3
Yellow poplar	1	-	6	-
Total	22	6	79	15

CONCLUSIONS AND SUMMARY

New sources of energy and chemical feedstocks are needed to replace expensive and rapidly diminishing pretroleum reserves. Woody biomass is expected to partially displace these raw materials now and in the future. Short rotation plantations, selected specifically for BTU yields or extractive content, may supplement forest residues and low quality stands to meet this objective.

Selections for short rotation plantations should be chosen and evaluated at an early age. Growth curves for individuals often change over time. Mild phenotypic selection in young, uniform stands should be used to select parent candidates that would be evaluated in open-pollinated progeny tests. The best individuals from the best families would form the breeding base for short rotation plantations.

Selection criteria for species and individuals to be included in these plantations will differ from those for trees selected for quality timber production. Most emphasis should be placed on proper species selection and matching species to sites. Individual traits of most importance are fast growth, followed by specific gravity and moisture content. High cellulose, lignin or extractive content may be selected for chemical production.

Wood is currently being utilized on a relatively small scale for energy and chemical production. As oil prices escalate, more emphasis will be focused on woody biomass for these uses. In the future, short rotation plantations may be established specifically for these end products. A breeding program for energy or chemicals should prove both feasible and economical.

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Genetic Variation in Sand Pine and Slash Pine for Energy Production in Silvicultural Biomass Plantations

D. L. Rockwood and L. J. Frampton[1/]

Abstract. - Sand pine and slash pine are candidate species for biomass plantations in Florida. Genetic variation within the species for energy production traits was examined to assess the increments possible through utilization of the most suitable families. Twenty-four sand pine families established near Archer, Florida, and 28 slash pine families established near Gainesville in high density tests were measured for growth traits, above ground biomass, moisture content, specific gravity, ash content, and calorimetric value.

Additional keywords: *Pinus clausa*, *Pinus elliottii*.

Energy production from woody biomass is receiving increasing emphasis in the United States, with silvicultural biomass plantations as one production alternative. In the Southeast, biomass production potential is very high, and in Florida, in particular, there are some unique opportunities to adapt promising species to the cultural conditions required for biomass generation.

Two species endigenous to Florida that are being examined in our Department of Energy project, Energy and Chemicals from Woody Species in Florida, are sand pine (*Pinus clausa* (Chapm.) Vasey) and slash pine (*P. elliottii* Engelm.). Sand pine is ideally suited to the large areas of dry, infertile, sandhills in the panhandle and peninsular portions of the state, and slash is well adapted to the extensive flatwoods common to north and central Florida.

Genetic improvement of these species has been conducted in the Cooperative Forest Genetics Research Program (CFGRP) at the University of Florida. For commercial forest plantations, sizable gains in volume and fusiform rust resistance of slash pine have been realized (Goddard and Rockwood 1978). Similar increases in volume production and other important traits of sand pine also appear possible (Rockwood and Goddard 1979).

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The potential response of these species to genetic improvement for the high-density, intensive culture regime required for silvicultural biomass plantations has not been previously evaluated. Important differences in the distribution of biomass, particularly its concentration in the stem, have been observed in Virginia pine (_P. virginiana_ Mill.) families planted at commercial spacing (Matthews et al. 1975). Significant genetic differences in dry matter production and distribution of that biomass were found in loblolly pine (_P. taeda_ L.) grown at 8' x 6' spacing and slash pine clones established at 15' by 15' (van Buijtenen 1978).

This paper presents findings concerning variation among sand pine and slash pine families grown under conditions that simulate biomass plantations.

MATERIALS AND METHODS

Field

Sand Pine

Some 50 Choctawhatchee sand pine (_P. clausa_ var. _immuginata_ Ward) families, derived from ortet open-pollinated seed collected from trees selected for superior growth rate and form, were established in a combination half-sib progeny test and seedling seed orchard near Archer, Florida. Planting was staggered over 3 years, 1973, 1974 and 1975. Families were planted two feet apart in 5 tree row plots spaced 15 feet apart in 20 replications.

In 1978, 24 families were sampled: 14 families in the 6-year-old planting, 6 in the 5-year-old planting and 9 in the 4-year-old planting. Up to 15 trees per family were sampled from the 4- and 6-year-old families and up to 6 trees per family from the 5-year-old families. Measurements included stem biomass (lbs.), combined branch and foliage biomass (lbs.), DBH (in.) (basal diameter on 4-year-old families) and total height (ft.). Additional sampling was performed on 5 of the trees sampled per family in the 4- and 6-year-old plantings and all of the trees sampled in the 5-year-old planting. Also, a basal stem disk and disks every 4 feet up the stem (except for 4-year-old trees) were retained for lab processing.

Slash Pine

Twenty-eight slash pine families in fertilizer tests established in 1971, 1972, 1973, and 1974 near Gainesville, Florida were sampled in 1978. The tests were randomized complete block designs involving three replications with split plots; fertilizer treatments were main plots and half-sib families (including a check lot) were sub-plots (5 tree row plots spaced 1 foot within rows and 4 feet between rows).

To make an initial assessment of biomass and energy production traits, one to three trees per family were sampled for the check seedlot and for 16 of the most promising families as determined by previous progeny evaluations. Stem biomass, combined branch and foliage biomass, DBH and total height were measured for all trees sampled. Retained for laboratory processing were a basal disk and disks every 4 feet up the stem.

Laboratory

Moisture content (percent) and specific gravity were evaluated for all of the slash and sand pine wood samples. The calorimetric value (BTU/lb.) and ash content (percent) were also determined for the wood of the basal disks of all the slash pine as well as all of the 6-year-old sand pine sampled.

All laboratory procedures were identical for the slash and sand pine samples. Determinations of moisture content, specific gravity, ash content, and calorimetric value were performed according to standards prescribed by the American Society for Testing and Materials (ASTM 1975 b, ASTM 1975 c, ASTM 1975 a, ASTM 1977) with one modification; burning of ash samples was done at 500°C.

RESULTS AND DISCUSSION

Sand Pine

Green weight biomass concentrations in the stem increased with age and were somewhat variable among families (Table 1). These concentrations, due to the 2' x 15' spacing, may not characterize the stem concentrations likely in similar aged but denser plantings.

Tree age and position in the stem influenced certain wood properties (Table 2). Moisture content decreased with tree age and increased with stem height at the same age; wood density, as somewhat shown by our data, can be expected to have the opposite relationships with age and stem position. Percent ash content was not discernibly related to position in the stem. BTU content was approximately 8600 per pound.

Table 1. Average and range of family means for percent of total above-ground green weight biomass in the stem of sand pine and slash pine.

Sand Pine				Slash Pine			
Age	No. of Families	Average	Range	Age	No. of Families	Average	Range
4	11	29.1	25.9-44.5	8	17	85.5	81.7-90.3
5	6	31.1	26.0-36.2	9	6	84.9	82.0-87.1
6	14	38.0	33.1-43.7	11	8	86.8	84.4-89.4

Table 2. Average wood properties and associated variation among families of Choctawhatchee sand pine stem wood as influenced by age and stem position.

	Stem Height			
Age	0'	4'	8'	12'
Moisture Content:				
4	194 176-206[1]			
5	181 160-208	216 198-230	223 178-240	
6	159 147-170**	197 168-235**	219 199-252	218 191-263**
Specific Gravity:				
4	.361 .342-.387			
5	.360 .310-.405	.324 .314-.333	.338 .297-.383	
6	.425 .407-.453*	.366 .317-.404*	.332 .292-.354	.338 .286-.276*
BTU:				
6	8573 8451-8695	8523 8398-8758	8580 8378-8721	8604 8474-8712
Ash:				
6	.0036 .0021-.0065	.0028 .0024-.0034	.0024 .0009-.0030	.0037 .0010-.0058

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[1] Range among family means. Significant variation among families noted by * and ** for the 5% and 1% levels, respectively.

Variation among families was observed for important stem wood characteristics at age 6 (Table 2). Moisture content differed by family at most stem positions, as did specific gravity. By utilizing high density, low moisture families, biomass plantations can be established that will yield more desirable stem wood.

Meaningful differences among these families were also noticed for critical growth traits. Fourth-year survival for the 26 families in the oldest planting averaged 67 percent while family means were as low as 20 percent and as high as 86 percent. Height differences at the same age were also significant with family means ranging from 4.1 feet to 10.5 feet.

No pertinent correlations among traits were detected. None of the wood properties were interrelated beyond certain implicit correlations among moisture content and specific gravity, and the growth traits were not related to each other. Further, no correlations among wood properties and growth traits were evident.

Improvement of Choctawhatchee sand pine for biomass production appears to be possible on several fronts. Volume production can be increased by selection for larger tree size in combination with emphasis on higher survival. Selection for wood properties can stress high wood density and low moisture content at the minimum. Characteristics of some of the better families are listed in Table 3.

Estimation of the possible stem wood yield of a sand pine biomass plantation in general, and the improvement due to using superior families in particular, is speculative for a variety of reasons. Although Choctawhatchee sand pine can tolerate a spacing of 2.5' x 3' for at least 17 years (Rockwood et al. 1979), evidence of its performance at a 2' x 2' spacing is lacking. However, the performance of jack pine at close spacing (Zavitkovski and Dawson 1978) in combination with inferences from the Archer plantings suggests that such a spacing is feasible for short rotation periods. Using the survival observed at Archer and the average tree size, volume, and weight observed by Rockwood et al. (1979) for young trees, a potential dry weight yield of 3.2 tons per acre per year was derived (Table 4).

Table 3. Characterization of some better performing sand pine families.

	Age 6						
	Basal Disk Wood Properties					Age 4 Growth	
Family	Moisture Content	Specific Gravity	BTU	Ash Content	Percent Biomass in Stem	Percent Survival	Height (Feet)
121	147	.437	8512	.0030	37.3	85.7	9.0
147	153	.435	8615	.0037	38.4	79.0	10.1
149	150	.431	8606	.0025	36.6	82.0	9.5
169	156	.435	8451	.0035	40.9	84.3	9.7
181	149	.453	8613	.0043	39.0	64.4	10.2
					Total Mean	67.0	9.1

Yields from utilization of better growing families may result in biomass production gains of nearly 24 percent. The projection for improved sand pine in Table 4 assumes a 10 percent increment for survival and 5.5 percent increases for height and dbh. Any improvements in wood properties would further add to the potential yield.

Biomass plantations of sand pine differ drastically from those proposed for other species in that very little cultural treatment is required. Other than minimal site preparation, most likely double chopping, management is very low intensity. No fertilization, irrigation, weed control, or other practices should be required in the majority of plantings. Further, the sites available for sand pine establishment are very low quality and not given to other agricultural uses.

The ideal rotation time for a sand pine biomass plantation may not necessarily be six years. Observations of older plantings (Rockwood et al. 1979) suggest that yields increase if stands are carried for several more years.

Table 4. Estimated stem biomass yields of unimproved and genetically improved sand pine and slash pine.

	Sand Pine - Age 6		Slash Pine - Age 8	
	Unimproved	Improved	Unimproved	Improved
Spacing	2' x 2'	2' x 2'	2' x 2'	2' x 2'
Survival	67%	74%	55%	69%
Trees/Acre	7,296	8,026	5,990	7,514
Mean DBH	2.0"	2.1"	2.0"	2.1"
Mean Height	14.0'	14.8'	16.5'	20.3'
Ft.^{3}/Tree	.206	.231	.221	.305
Ft.^{3}/Acre	1,503	1,854	1,325	2,292
Ft.^{3}/Acre/Year	251	309	189	286
Lbs./Tree	5.25	5.96	5.90	9.04
Tons/Acre	19.2	23.9	17.7	34.0
Tons/Acre/Year	3.2	4.0	2.2	4.2

Slash Pine

The concentrations of green weight biomass in slash pine stems were considerably higher than those of sand pine (Table 1). The closer spacing of the slash pine produced great uniformity in the stem percentages, as very little variation among families was evident. The differences in concentrations from age 8 to age 11 were minimal; the age at which stemwood percentages first exceed 80 percent could not be determined from our sampling.

For the one age at which within tree variation for wood properties was evaluated, expected relationships between stem height and wood moisture content and specific gravity were observed (Table 5). With the exception of basal specific gravity, wood density decreased with tree height. Moisture content increased with height.

Table 5. Average wood properties and associated variation among 17 8-year-old slash pine families for stemwood.

Stem Height	Wood Property Moisture Content	 Specific Gravity	 BTU	 Ash Content
0'	105	.469	8509	.0028
	89-142[1/]	.414-.516	8200-8790	.0019-.0042
4'	109	.492		
	93-148	.421-.522		
8'	124	.457		
	89-139	.397-.512		
12'	136	.424		
	108-159	.365-.453		
16'	152	.398		
	112-187	.361-.440		
20'	181	.355		
	140-216	.281-.420		
24'	185	.339		
	127-247	.296-.326		

[1/] Range among family means. Family variation was not significant for any trait.

The wood properties of 8-year-old slash pine were generally more favorable than those of 6-year-old pine. Wood density was typically 10% higher and moisture content 10% lower for slash. Ash contents were similar. BTU yields may be slightly lower for slash pine.

As with the sand pine, there were no meaningful correlations noted among the wood properties, but no significant variation among the slash pine families was detected. For certain data, large differences among family means were noted, but may not have been detectable due to the lower number of observations in our sampling.

Variation among families for growth traits was evident (Tables 6 and 7). Survival and height differences were significant by age 3 in all plantings. Families differed for dbh at age 7. Families generally surpassed check lot performance by age 7.

Growth traits were not interrelated nor were they associated with wood properties.

Increased slash pine biomass production can be achieved by utilizing better growing families and capitalizing on families with more desirable wood properties. The projections in Table 4 for unimproved stock are based on the performance of

Table 6. Growth performance of slash pine families in four high density plantings.

Planting	Age	Percent Survival	Height (Feet)
0-14	3		4.3 3.4-5.3[1]
0-18	3		6.3 5.2-7.5*
0-29	3	95 77-100*	6.4 5.5-8.9*
0-36	3	65 28-95*	7.4 5.9-8.9*
	7	55 25-86*	16.5 11.8-22.9*

---

[1] Range among family means. Significant variation at the 5% level as noted by *.

Table 7. Comparison of various classifications of slash pine families at age 7.

Trait	Check	All Families	Top 15 Families
Survival (percent)	46	55 25 - 86	69 58 - 86
Height (feet)		16.5 11.8 - 22.9	20.3 18.8 - 22.9
DBH (inches)	1.7	2.0 1.5 - 2.5	2.1 2.0 - 2.4

the families in the 8-year-old planting in combination with previously derived tree volume and weight estimates (Goddard and Strickland 1968). Due to a lower survival rate than the sand pine, an unimproved slash pine biomass plantation, in spite of a somewhat larger tree size and heavier wood, might be expected to produce a lower dry weight yield.

Use of the very best slash pine families can substantially increase production (Table 4). In the CFGRP, a much larger pool of genetic material may be exploited, and consequently greater increments in survival, height, and wood density can be anticipated. By implementation of the top 15 families as a characterization of the greater potential, a possible dry weight yield of 4.2 tons per acre was projected.

CONCLUSIONS

Choctawhatchee sand pine and slash pine have potential as biomass species for different sites in Florida. Projected yields for the species are comparable to other candidate species (Conde and Huffman 1978). Sand pine can be utilized on extensive areas of non-agricultural land in north and central Florida. Slash pine would be suitable to a larger area of wetter forest lands in north and central Florida. Both species, particularly sand pine, would require relatively low intensity management relative to regimes for other biomass candidates. Utilization of selected families promises to increase yields primarily through higher volume production and secondarily by better wood properties.

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COMPARISON OF GROWTH AND VOLUME PRODUCTION OF SLASH AND LOBLOLLY PINE TEST PLANTATIONS ON TWO PLANTING SITES

Ernest M. Long[1]

Abstract.--In progeny test plantings established on two separate test areas in East Texas, adjacent plantations of loblolly and slash pine were compared after 10 years. Loblolly pine produced about 22 percent more volume than comparison slash pine plantations. Survival of loblolly pine was slightly higher than slash pine. Infection and mortality attributed to fusiform rust was also higher in slash pine than in loblolly pine plantations.

Additional keywords: *Pinus taeda*, *Pinus elliottii* var. *elliottii*, productivity, growth and yield, species comparison

The most commonly planted pine species in East Texas are slash pine (*Pinu elliottii* Engelm. var. *elliottii*) and loblolly pine (*Pinus taeda* L.). Lobloll pine is planted throughout the eastern part of the state from Galveston Bay north to the state line and west into the post oak belt on the western edge of the natural range of loblolly pine.

Slash pine is not a native species in Texas but it has been planted in the state for over 50 years. Most slash pine plantings are established in the coastal plain in the southeast corner of the state and inland up to 100-150 miles from the Gulf of Mexico.

Differences in productivity between slash and loblolly pine should be considered in long term forest management planning. However, reports on comparative growth and yield from slash and loblolly pines are somewhat contradictory. Shoulders (1970) indicated that loblolly and slash pines in central Louisiana grew about the same rates from ages 23 to 38 when initial difference in diameter were allowed for. In 1977 Shoulders compared 15-year-old slash in central Louisiana and concluded that loblolly and slash pine appeared to be equally suited for short rotation on coastal plain soils in central and south Louisiana. Cole (1973) reported that loblolly pine was significantly more productive than slash pine in Florida, Georgia, and South Carolina on planting sites in the lower and middle Atlantic coastal plain and Piedmont region. In these test plantings volumes averaged about 49 percent higher for loblolly pine than for slash pine.

MATERIALS AND METHODS

All seedlings, including controls, were grown at Indian Mound Nursery near Alto, Texas. All test material was randomized and replicated in the nursery beds. Nineteen or more families were included in each test planting.

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Progeny test plantations had eight or more replications of randomized four tree row plots. The 1967 plantings had 12 replications, a total of 1200 trees, for both loblolly and slash pine plantations at both locations. The 1968 slash pine plantings used the same design as the 1967 plantings. A slightly different design was used for the loblolly plantings in 1968 because of low seed germination in some families.

Two plantations, one slash pine and one loblolly pine, were established at each planting area during 1967 and 1968. Thus a total of eight plantations at two locations were available for comparison.

The slash pine plantings were from controlled pollinated crosses between seed orchard trees selected for good growth and form. Since slash pine is not native to Texas all slash pine selections were from plantations established in East Texas. Information on provenance was unavailable for some of the parent plantations.

Loblolly pine plantations established during 1967 were from crosses of seed orchard trees selected for good growth and form from native stands throughout East Texas. The 1968 loblolly plantations contained both open-pollinated and controlled pollinated drought resistant selections from the extreme western edge of the natural loblolly range.

Four plantations were established on the Spurger test site in Tyler County - about 75 miles inland from the Gulf of Mexico. The site is level coastal plain with about 55 inches of annual rainfall. The soil has good internal drainage and slow surface drainage. Overall, the site is typical of many areas in the coastal plain where slash pine is being extensively planted.

Comparison plantings were made at Pine Valley in San Jacinto County about 100 miles northwest of the Gulf of Mexico. The site is slightly hilly with good surface drainage and poor internal drainage. Rainfall is about 45 inches annually. Slash pine is also planted widely in this area.

On both planting sites, slash pine and loblolly pine plantations were either planted adjacent to each other or as close as topography and soil variations would permit.

Height and diameter of all trees were measured at five and ten years. Incidence of infection by fusiform rust (Cronartium fusiforme Hedgc. & Hunt) was recorded along with height and diameter measurements. Form evaluations and specific gravity determinations were made at ten years.

Comparisons between slash and loblolly pine plantation growth and volume production was analyzed as unpaired observations (Steele and Torri 1960). Percentage data used in analysis was converted by arcsine $\sqrt{\text{percent}}$ transformation.

RESULTS AND DISCUSSION

Volume

In all comparison plantings loblolly pine produced more volume than slash pine. Overall, loblolly pine produced an average of over 22 percent more cubic volume than slash pine after 10 years. In three of the four pairs of plantations loblolly pine produced significantly more volume than slash pine. In the fourth pair of plantations loblolly pine produced more volume than slash pine but the difference was not statistically significant.

Survival

At ten years loblolly pine averaged about 87 percent survival over all plantations while slash pine averaged about 80 percent survival. There was no significant difference in survival when all plantations were grouped together for analysis. When comparisons were made between pairs of plantations, two had significantly higher loblolly pine survival, while one pair had significantly greater slash survival and the fourth pair had no significant difference in survival.

Differences in survival between loblolly and slash pine resulted in part from losses of slash pine to fusiform rust. The amount of infection by fusiform rust appeared to be greater on slash pine than on loblolly pine and to have caused more mortality of slash pine than loblolly pine.

Basal Area

Basal area of the loblolly pine plantation averaged about 18 square feet per acre more than slash plantations. Survival would be expected to influence basal area but it was not the only factor which caused differences. For example, in adjacent plantings where slash pine had a survival rate of over five percent more than loblolly pine the latter had about 21 square feet per acre more basal area than the former. In all comparisons of pairs of plantations loblolly pine had significantly more basal area than slash pine.

Height

In the four comparison plantings slash pine had significantly greater height than loblolly pine in two, was not significantly taller in the third, and was shorter in the fourth. When all plantations are compared there was no significant difference in height growth. The differences in height ranged from .2 percent up to about 10 percent. The average difference between all comparison plantings was about three percent in favor of slash pine.

Diameter

Loblolly pine had a greater diameter than slash by an average of about six percent for all plantations. In two of the four comparison plantings loblolly pine had signficantly greater diameter than slash pine. In the other two plantings the difference was not significant.

In the 1978 plantings at Pine Valley competition from wild pine seedlings and hardwood sprouts influenced the growth rates of both slash and loblolly pine in test plantations. Differences in growth potential were obscured by this competition. In the other six plantations competition with non-planted trees was light to moderate. (Volume, survival, basal area, height, and diameter data are summarized in table 1).

Table 1.--Loblolly pine and slash pine plantation means at 10 years.

	Location and Year			
	Pine Valley		Spurger	
	1967	1968	1967	1968
Volume (M^3ha yr)				
Loblolly	5.50 a[1]	4.07 a	10.49 a	8.89 a
Slash	4.66 b	4.06 a	8.53 b	6.34 b
Height (M)				
Loblolly	8.70 a	7.59 a	11.26 a	10.12 a
Slash	8.72 a	8.37 b	11.08 b	10.64 b
Diameter (CM)				
Loblolly	11.44 a	9.46 a	13.44 a	12.27 a
Slash	11.01 b	9.55 b	12.00 b	11.42 b
Basal Area (Sq.ft.)				
Loblolly	82.6 a	70.1 a	121.8 a	114.8 a
Slash	72.8 b	63.4 b	100.7 b	78.0 b
Survival (Percent)[2]				
Loblolly	61.54 a	76.31 a	64.90 a	75.70 a
Slash	60.19 a	66.58 b	68.95 b	58.66 b

[1] Pairs of plantations with different letters differ at the .05 level of significance.

[2] Survival data converted by arcsine $\sqrt{\text{percent}}$ transformation.

CONCLUSION

The differences in growth between loblolly and slash pine in these plantations indicates that planting slash pine on these sites would offer no particular advantage over loblolly pine but would result in significantly less volume production.

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INHERITANCE OF SPROUT GROWTH IN AMERICAN SYCAMORE (*Platanus occidentalis* L.)

Charles D. Webb[1] and Roger P. Belanger[2]

Abstract.--A 4-year-old progeny test of 64 wind-pollinated sycamore families was harvested and stumps were permitted to sprout. After four years, sprouts were measured and heritabilities calculated for growth. The plantation averaged 2.49 sprouts per clump; dominant sprouts averaged 7.89 m tall and 5.21 cm in diameter at 30 cm. Total dry weight production of the 0.23 ha plantation was 8,284 kg/ha/year during the sprout rotation. Narrow-sense heritabilities were: height, 0.16; diameter of dominant sprout, 0.20; number of sprouts per clump, 0.05; sprouting capacity expressed as total dry weight of all sprouts in a clump, 0.17. Family averages in dry weight per clump varied widely: the best family was 46% greater than the plantation average, the poorest family equaled only 48% of the plantation average.

Additional keywords: Coppice, additive variance, heritability, hardwoods, short rotations, silage sycamore, Georgia, energy plantations, whole-tree utilization.

In the 13 years since the "silage sycamore" concept was proposed (McAlpine *et al.* 1966), considerable attention has been given to the concepts of coppice regeneration of hardwoods with complete tree utilization for fiber products or energy production. Numerous studies have shown that application of this concept can produce high yields of fiber very soon after plantation establishment (Wood *et al.* 1976; Steinbeck and Brown, 1976). Young (1967) demonstrated that dense natural stands of hardwoods in the Northeast can also produce high yields of wood fiber. Utilization studies have reported generally acceptable paper and other reconstituted wood products can be manufactured from relatively small, whole trees (Steinbeck and Brown 1976). Economic analyses have shown that the concept is most profitable for fiber products with good sites, wide spacing and cutting cycles of 4 or 5 years (Dutrow and Saucier 1976).

Informal observations on clones of sycamore in a nursery revealed obvious differences among clones in growth and sprouting characteristics. Certain clones tended to have one or two dominant sprouts on each stump, while other clones characteristicly had 3 to 6 sprouts per clump competing for dominance. In a breeding program, the size and nature of genetic variation in sprouting characteristics under intensive culture would be important. The present study was developed to quantify heritabilities of key expressions of sprouting in young sycamore.

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METHODS

In 1968, seedlings of 64 wind-pollinated families were planted in an overflow bottom of the Oconee River in Greene County, Georgia, at a spacing of 1.2m x 1.2m (4'x 4') in 4-tree plots. Weed competition during the first year was controlled by mowing. Fertilizer was applied twice during the first four years, once as 12-12-12, once as ammonium nitrate. After four growing seasons, the plantation was clearcut to a stump height of 15 cm (6"). Stumps were permitted to sprout, and again after four growing seasons the plantation was measured. Measurements included height and diameter of each major sprout and a count of the number of sprouts originating from each stump. Using regression equations developed by Saucier, *et al*[1], estimates were developed for all sprouts in each clump for total dry weight and total green weight. For a description of methodology of the earlier phase of the study, genetic assumptions and limitations, see Webb, *et al*. 1973.

Table 1.--The analyses of variance and construction of heritabilities

Source	df	E(ms)
Replication	5	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2 + f\sigma_r^2$
Family	63	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2 + r\sigma_f^2$
RxF	315	$\frac{\sigma_w^2}{k} + \sigma_{rf}^2$
Total	383	
Within plot	993	$\frac{\sigma_w^2}{k}$

k = harmonic mean number of trees per plot = 2.8098

Assumption: half-sib family component $\sigma_f^2 \hat{=} \frac{1}{4}\sigma_A^2$

Narrow sense heritability:

$$h^2 = \frac{4\sigma_f^2}{\sigma_w^2 + \sigma_{rf}^2 + \sigma_f^2}$$

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[1] Personal communication, J. Saucier, A. Clark III, and R.G. McAlpine, USDA Forest Service, Southeastern Forest Experiment Station, Athens, GA.

RESULTS

The general growth of sprouts over the entire plantation was excellent. After four growing seasons, height averaged 7.89 m (25.9') and diameters of dominant sprouts at 30 cm (1') averaged 5.21 cm (2.05"). The plantation produced a total of 33,139 kg/ha (14.8 T/acre), or an average annual rate of 8,284 kg/ha/yr. (3.7 T/acre/yr). Wind-pollinated families demonstrated highly significant differences in sprout growth when expressed in terms of height, diameter, dry weight and green weight (table 2).

Table 2.--Key statistics summarizing inheritance of sprouting capacity.

Statistic	Height	Diameter	Total dry weight	Total green weight	Number of sprouts per clump
Heritability, narrow-sense	0.16	0.20	0.17	0.17	0.05
Family F-test[a]	1.58**	1.85**	1.74**	1.74**	1.37 N.S.
Variance components					
Half-sib family, σ_f^2	1.0400	0.020623	2.9449	18.5619	0.020039
Rep. x family, σ_{rf}^2	3.0870	0.016070	0.6399	4.6266	0.697314
Within plot, σ_w^2	21.7456	0.365852	65.0196	407.3690	0.813578

[a] df 63,315

The expression of sprouting capacity that had the widest range of variability was total dry weight of all sprouts in a clump. This is a function of height, diameter, and number of sprouts per clump. The individual clump variation in dry weight ranged from less than 2 kg per clump to over 23 kg per clump (fig. 1). Family averages ranged from a low of 2.58 kg (5.68 lb) per clump to a high of 7.18 kg (15.84 lb) per clump. Stated another way, the poorest family in the plantation produced dry matter at a rate equal to only 48 percent of the plantation average. However, the best family produced dry matter at a rate 46 percent greater than the plantation average.

When sprouting was expressed in number of sprouts per clump, the total range of variability was very narrow, 6 sprouts per clump or less (fig. 2). The F-test for families was non-significant, and narrow-sense heritability was only 0.05 (table 2). However, informal observation of sycamore clones in the nursery suggested a high broad-sense heritability for number of sprouts per clump. This apparent descrepancy suggests that the factors controlling this aspect of sprouting express dominance rather than additive gene action.

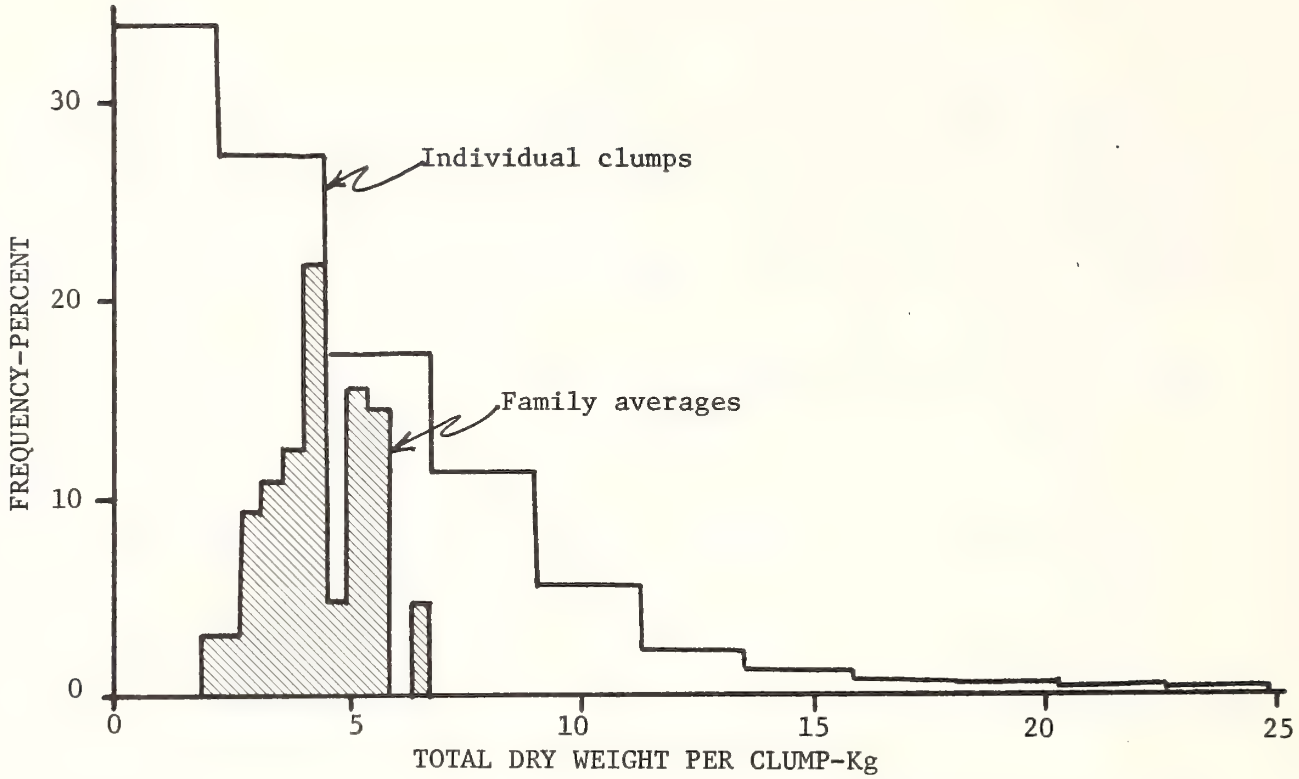

Figure 1: Total dry weight per clump: frequency distribution of 1215 sprout clumps compared with 64 family averages.

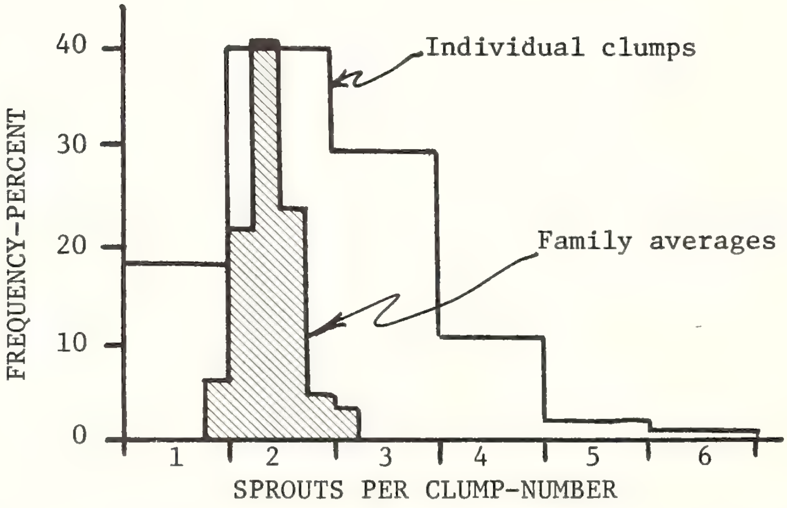

Figure 2: Number of sprouts per clump: frequency distributions of 1215 sprout clumps compared with 64 family averages.

CONCLUSIONS AND RECOMMENDATIONS

This small plantation, in a single location, again demonstrates the capacity of sycamore sprouts to yield large quantities of usable dry matter on a good site under intensive culture on short rotations. Furthermore, there is adequate additive genetic variance in the growth capacity of sprouts to reward an applied breeding program designed to increase productive capacity under intensive culture. More work, however, is needed to define the relative importance of additive genetic variance and dominance variance in factors affecting competition among sprouts originating from the same stump.

Once a decision is made concerning the proposed rotation length, 4 to 6 years versus 10 to 15 years, then decisions can be made about relative emphasis on number of sprouts per clump, total dry weight per clump, and upon using seedlings or cuttings. This plantation of sprouts is now 6 years old; competition is becoming very intense and smaller sprouts are dying out.

The following recommendations are offered for an applied breeding program: If rotations are projected to be short, 4 to 6 years, selection should favor those families that maximize total dry weight per clump, and seedlings can be used to establish operational plantations. These families will probably have an above average number of sprouts per clump. However, if rotations are projected to be longer, 10 to 15 years, selection should favor those families that maximize total dry weight, but on only 1 or 2 stems per clump. This strategy would minimize loss of production through mortality of suppressed sprouts. To achieve this sprouting pattern, it may be necessary to plant cuttings instead of seedlings to utilize the apparent broad-sense heritability of number of sprouts per clump.

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